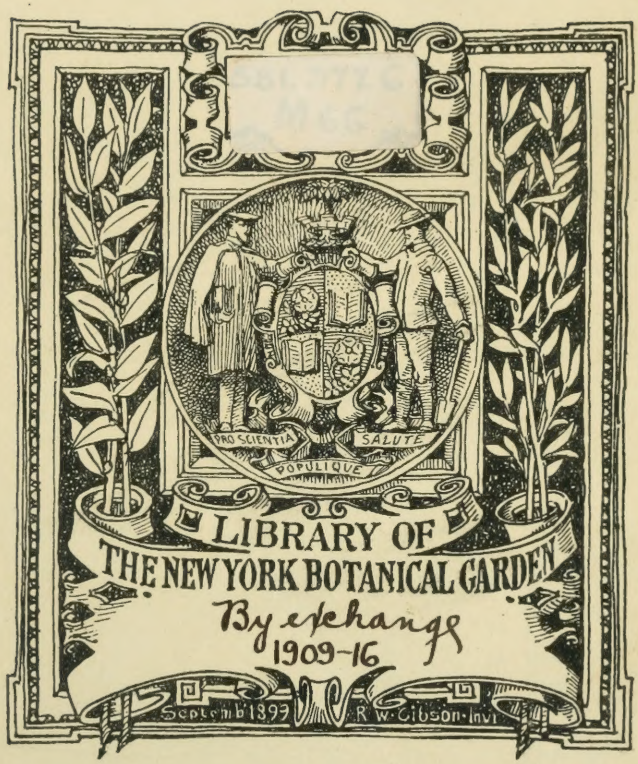
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MINNESOTA BOTANICAL STUDIES

GEOLOGICAL AND NATURAL HISTORY SURVEY OF MINNESOTA
FREDERIC E. CLEMENTS, *State Botanist*

MINNESOTA
BOTANICAL STUDIES

Vol. IV

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VII

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Part IV, pp. 333-491, Pl. XLI-XLIX Title page, table of contents and index	Sept. 20, 1916

GEOLOGICAL AND NATURAL HISTORY SURVEY OF MINNESOTA
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Minnesota Botanical Studies

PART I.
VOLUME IV.

University of Minnesota
Minneapolis
June 10, 1909

CONTENTS.

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C. OTTO ROSENDAHL.

In a preliminary note published in Science [1] the writer has called

MINNEAPOLIS, June 10, 1909

The present number of the "Minnesota Botanical Studies" is the first one to be issued since 1904. On account of the time that has intervened, this number is issued as part 1 of volume IV. The three preceding parts will constitute volume III, for which index and title page will be furnished at an early date. Owing to the necessity for limiting the edition, copies of the "Minnesota Botanical Studies" will hereafter be distributed free only to institutions, departments of botany and working botanists.

FREDERIC E. CLEMENTS,
State Botanist.

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I wish to express my obligations to Dr. Harold L. Lyon and Mr. W. H. Lippold, both lately connected with the Department of Botany of the University of Minnesota, for suggestions and assistance in the beginning of this work. I am also under obligation to Miss Alice Misz for help in the tedious work of preparing the drawings for the accompanying plates.

[1] A Preliminary Note on the Embryogeny of *Symplocarpus foetidus*. C. Otto Rosendahl. Science. Vol. 23. April 13, 1906. p. 590.

[2] Morphology of *Spathyema foetida*. James Ellis Gow. Botanical Gazette. Vol. 43, 2, p. 131. 1907.

1. EMBRYO-SAC DEVELOPMENT AND EMBRYOLOGY OF SYMPLOCARPUS FOETIDUS.

C. Otto Rosendahl.

In a preliminary note published in Science [1] the writer has called attention briefly to some of the main features in the development of the embryo of the common Skunk Cabbage (*Symplocarpus foetidus*). The contemplated paper setting forth the facts more in detail, was for various reasons unduly delayed, and in the meantime a study of the "Morphology of Spathyema foetida" appeared in the Botanical Gazette.[2] This paper dealt largely with the development and structure of the micro- and macrosporangia, but did not take up the development of the embryo beyond the 4-celled stage. Some of the observations on the development of the embryo-sac recorded in Mr. Gow's paper differ so markedly from those made by the writer that it seems worth while to record them for comparison and in the hope that further study of the subject may be stimulated thereby

The material upon which these observations are made was collected during the fall months from September to November until the ground was frozen, and in the spring from the time the frost left the ground until June. Various killing and fixing media were used, of which chrom-acetic acid proved the best. Safranin-Gentian Violet and Haidenhain's Iron Alum Haematoxylin gave the best staining results.

I wish to express my obligations to Dr. Harold L. Lyon and Mr. W. H. Lippold, both lately connected with the Department of Botany of the University of Minnesota, for suggestions and assistance in the beginning of this work. I am also under obligation to Miss Alice Misz for help in the tedious work of preparing the drawings for the accompanying plates.

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The thick, upright, underground stem of Symplocarpus foetidus gives rise to a varying number of inflorescences each year. The winter bud is protected by 2-3 scale leaves. The inflorescences of the season are produced among the sheathing bases of these. Usually a limited number of them (1-3) come to maturity each year while the others remain arrested. Growth and development of the floral organs is very slow as shown by the fact that inflorescences collected in September and which are to blossom out eighteen to twenty months later, already show the spathe and spadix well differentiated and the rudiments of the flowers laid down (Fig. 1, Pl. I). In this stage of development the floral branch passes the winter and it is not until the following summer, the one previous to the spring of blossoming, that the ovules are developed.

In nearly all cases the ovary is one-chambered, with but one ovule in the chamber (Fig. 2, Pl. I). This is orthotropous and pendant from the upper part of the cavity. Occasionally two chambers are found with an ovule in each, or more rarely with more than one in each (Fig. 3, Pl. I). This is not remarkable in view of the generally inconstant character of the gynaeceum among the Aroids.

In the fully mature ovule two integuments are present. The outer one of these very seldom comes more than half ways up the nucellus; the inner either does not cover the end of the nucellus, thereby forming a collar around it (Fig. 22, Pl. II), or else it covers it completely, leaving only a narrow micropylar passage (Fig. 33, Pl. III). In material collected about the middle of September the inner integument is beginning to form, and the archesporium shows as a somewhat enlarged, densely protoplasmic cell (Fig. 4, Pl. I). It is covered at this stage by a double layer of cells (Fig. 30, Pl. III).

A tapetal cell is cut off from the archesporium by means of a periclinal wall and in this cell anticlinal walls soon follow (Fig 4, Pl. I and Fig. 31, Pl. III). The archesporium, by virtue of a periclinal division of the tapetal cell, as well as several periclinal divisions of the originally single superficial layer of the nucellus, becomes somewhat deepseated (Fig. 4-5, Pl. I). In this stage of development the megasporangium passes the winter season at least in the region around Minneapolis where the material for these observations was collected. An examination of figures 4 and 5 which are made from material collected respectively in late November and early April,

shows that during a normal winter season there is practically no growth taking place between these two dates. In the latter figure the archesporial cell has enlarged somewhat and the nucleus is preparing for division. According to the observations of Mr. Gow the plants behave quite differently in New Jersey, where no trace of the inner integument is to be noted before the latter part of February, and the archesporium does not become recognizable before the first or second week of March.

Upon resuming growth in the spring the successive stages in the development of the embryo-sac follow each other rapidly. The single archesporial cell (Fig. 4-5, Pl. I and Fig. 30-31 Pl. III) becomes the spore-mother cell, which by two successive divisions gives rise to *four* megaspores, and not *three* as recorded in the above mentioned observations (Fig. 6-10, Pl. I). The position of the four megaspores with relation to each other is not always the same in different ovules. In most cases the two innermost ones lie in the long axis of the ovule, while the two outermost lie transversely (Fig. 8-9, Pl. I). This arrangement of the four megaspores is very likely what has given rise to the erroneous statement that only three spores are present, for if the section happens to strike through the ovule in such a way that the two outermost spores lie over each other it is easy to overlook one of them (Fig. 9, Pl. I). More rarely all four spores are arranged in a straight row (Fig. 10, Pl. I). At this stage in the development of the megasporangium the inner integument has pushed forward but does not cover the end of the nucellus. The outer integument is just beginning to appear in the form of a slight swelling about on a level with the base of the nucellus.

It seems probable that all four spores germinate. However this stage in the development has not been observed in a sufficiently large number of embryo-sacs to fully substantiate the statement. The nuclei of three spores have been seen to be in a state of division (Fig. 11, Pl. I). The fourth, one of the outer or micropylar ones, still remaining undivided, although showing signs of preparing for division. (In the figure only two dividing nuclei are shown, the third, being in a deeper plane and obscured by the undivided one, is in such a position that it could not be drawn).

The successive nuclear divisions in the development of the embryo-sac from the spore evidently follow each other with great rapidity, for from a very large number of slides examined, the two- and

four-celled stages were not encountered. On the other hand the stage where four nuclei are closely grouped at either end was often found (Fig. 12, Pl. I). The mature embryo-sac varies considerably in form and size but is generally twice as long as wide and oval in outline. The two polar nuclei behave in the usual way, approaching and fusing near the middle of the sac (Fig. 17, Pl. I).

In the micropylar end of the embryo-sac are found at this stage of its development a number (4-6) of more or less darkly staining, irregular bodies. They lie closely grouped just outside the four nuclei and are evidently the remnants of the other germinating megaspores (Fig. 12-13, Pl. I). They persist only for a short time and disappear when the fertilized ovum begins to divide. The presence and position of these bodies seem to indicate that the innermost megaspore is the one that gives rise to the embryo-sac. The egg and synergids enlarge and elongate and the usual vacuolate character of these cells becomes evident (Fig. 13, Pl. I).

In the process of fertilization the pollen tube makes its way through the micropyle and penetrates the nucellar tissue, sometimes in a direct manner, at other times more or less irregularly, and enters the embryo-sac (Fig. 33, Pl. III). In no case, however, have the sperm cells been observed nor actual nuclear fusion seen. Presumably it takes place in the usual way.

The ovum begins to enlarge somewhat and the first division in the young embryo is transverse to the long axis of the embryo-sac (Fig. 14, Pl. I). Other divisions follow in the same plane as the first, and a row of three to four cells is built up before anticlinal walls appear (Fig. 15, Pl. I). These latter proceed from the tip towards the base. The synergids remain during the first stages of embryo formation but soon begin to break down and disintegrate (Fig. 14-15, Pl. I).

In the development of the endosperm a brief period of free cell formation (Fig. 14-16, Pl. I) is followed by the appearance of cell walls, whereby a tissue is built up throughout the embryo-sac (Fig. 20, Pl. I). The endosperm nuclei as they are formed distribute themselves more or less irregularly throughout the embryo-sac and the walls appear about simultaneously between all the nuclei. The endosperm grows rapidly and soon begins to encroach upon the remnants of the nucellar tissue (Fig. 37, Pl. III) then upon the inner integument (Fig. 35, Pl. III), and finally begins to push back into

the base of the ovule (Fig. 36, Pl. III). The inner integument is quickly consumed, and the outer meets the same fate as soon as the growing endosperm comes in contact with it. Thereupon the basal portion of the ovule is attacked.

The early behavior of the antipodal cells seems subject to some variation. In embryo-sacs where no embryo or endosperm development takes place, and this happens to be the case with a large number of the ovules examined, the antipodal cells begin to shrink and disintegrate before the egg apparatus shows any such signs. In rare cases on the other hand the antipodals increase greatly in size before any signs of fertilization become evident (Fig. 18, Pl. I). As soon as the embryo begins to segment and endosperm to form, the normal behavior of the antipodal cells is to begin dividing and to show signs of becoming active. In such cases they stain deeply and the nucleus possesses usually a number of nucleoli (Fig. 16, Pl. I).

After the endosperm tissue has been built up by the formation of cell walls a number of large cells with greatly enlarged nuclei become differentiated in the antipodal region (Fig. 21, Pl. II and Fig. 36, Pl. III). It has been impossible to trace the origin of this tissue directly by following the actual division of the original antipodal cells, yet there seems little doubt that it is derived in this way. In many cases no sharp line of demarkation can be noted between these cells and the endosperm tissue, still this does not preclude the possibility of their being formed by division from the antipodals. The enormous size of these cells and the greatly enlarged nuclei, give them an entirely different appearance from the normal endosperm cells (Fig. 21 and 23, Pl. II). Furthermore a varying number of deeply staining bodies are found in the cytoplasm outside the nucleus and these are lacking throughout the endosperm tissue (Fig. 23, Pl. II). This antipodal tissue is built up rather later than the endosperm and in most cases seems to invade the latter (Fig. 21, Pl. II and Fig. 36, Pl. III).

The first stages in embryogeny were briefly described above (Fig. 14-15, Pl. I). In the more or less cylindrical pro-embryo made up of a row of three or four cells, anticlinal or longitudinal walls first appear in the anterior cell. These divisions are followed by further transverse and longitudinal ones with the result that the pro-embryo becomes more or less club-shaped (Fig. 27, Pl. II). In

the meantime all the cells of the original row of three or four cells divide lengthwise, whereby a short, more or less massive suspensor is differentiated at the posterior end (Fig. 27 and 24, Pl. II). As growth and development of the pro-embryo proceeds, it changes from club-shaped to pyriform or ovoid (Fig. 38, Pl. III). The short suspensor is in intimate contact with the endosperm as long as the latter is intact (Fig. 19, Pl. I) but as the pro-embryo rounds off more and more and becomes larger, the suspensor begins gradually to disappear.

The first indication of leaf and plumule differentiation is to be noted in the form of a small depression which forms on one side of the ovoid cotyledon (pro-embryo) close to the suspensor (Fig. 29, Pl. II). By the time this depression first becomes evident the pro-embryo is already a massive body numbering thousands of cells. The depression deepens and becomes a groove (Fig. 25, Pl. II) by the surrounding tissue growing up from below and from both sides towards the middle. The two edges come close together, thereby covering up the developing leaf rudiments, and form a narrow slit in the surface of the pro-embryo, near the suspensor (Fig. 26, Pl. II). The first leaf arises on the axial side of the groove, appearing at first like a small protuberance. Immediately below it the apex of the stem differentiates (Fig. 39, Pl. III), and on the other side of this a second leaf is formed alternating with the first. The overlapping leaf rudiments are more or less sharply bent over the stem apex and in sectional view appear somewhat V-shaped (Fig. 40, Pl. III).

By this time the pro-embryo has assumed an almost spherical shape, and practically all traces of the suspensor have disappeared. The radicle begins to differentiate just below the suspensor region. The root-cap appears as a slight elevation and beneath it the plerome is distinctly traceable by the presence of a group of trachieds (Fig. 40, Pl. III). The axes of the plumule and the radicle form a somewhat acute angle with each other, the one being bent back upon the other (Fig. 40, Pl. 3). While these structures are being developed the embryo completely devours the endosperm, the two integuments, and the basal portion of the ovule. No ovular tissue is ultimately left except a remnant of the base of the funicle which remains in more or less intimate contact with the slightly indented forward end of the embryo. The embryo therefore comes to lie

naked in the cavity of the ovary without any protective layers or seed coats (Fig. 28, Pl. II).

SUMMARY.

1. The inflorescences of *Symplocarpus foetidus* develop very slowly and the rudiments of the flowers are distinguishable from eighteen to twenty months before the time of blossoming. The ovules are developed during the late summer and fall months of the year previous to blossoming. In most cases the ovary is one-chambered, with only one ovule in each chamber. The ovule is orthotropous and pendant from the upper part of the cavity. Occasionally two chambers are found with one or more ovules in each.

2. A single archesporial cell is differentiated which becomes the spore-mother cell. This, by two successive divisions, gives rise to four megaspores. In most cases the two megaspores towards the chalaza end lie in the long axis of the ovule, while the two towards the micropylar end lie transversely. All four spores germinate, the innermost one giving rise to the embryo-sac, the others breaking down.

3. The first divisions of the oospore are transverse and a row of three or four cells is built up before anticlinal walls appear.

4. In the development of the endosperm a brief period of free cell formation is followed by the appearance of cell walls whereby a tissue is built up throughout the embryo-sac. It grows rapidly and encroaches upon the inner and outer integuments, and finally begins to push back into the basal tissue of the ovule.

5. The antipodal cells give rise to a tissue made up of a considerable number of cells with greatly enlarged nuclei.

6. The pro-embryo as it grows becomes at first club-shaped and later on pyriform or ovoid. A short suspensor, consisting of several rows of cells, is formed. Upon one side of the pro-embryo, near the suspensor, a small depression appears, which later deepens into a groove. On the axial side of this groove the leaves and plumule are differentiated.

7. The embryo, during its growth, completely consumes the endosperm, together with the integuments and other ovular tissues. Consequently it comes to lie practically naked in the cavity of the ovary and hence no real *seeds* are produced in *Symplocarpus foetidus*.

Explanation of Plates.

The drawings were made with the aid of a camera lucida and reduced nearly one-half. The magnifications indicated are those to which they were originally drawn before reduction. The figures on plate III, (numbers 30-40 inclusive), are photo-micrographs and are reduced the same as the drawings.

Fig. 1. Longitudinal section through the inflorescence, about 19-20 months before blossoming. × 16.

Fig. 2. Longitudinal section through ovary showing single ovule. × 82.

Fig. 3. Longitudinal section through ovary showing several ovules. × 82.

Fig. 4. Longitudinal section of ovule showing archesporial cell and "tapetal" layer to the outside. Several periclinal divisions in the micropylar end of the nucellus have taken place. Archesporial or spore-mother cell in a stage of synapsis. Fall condition. × 630.

Fig. 5. Spore-mother cell shortly after growth has been resumed in the spring. Nucleus showing spireme. × 840.

Fig. 6. First division of spore-mother cell. × 840.

Fig. 7. Second division of spore-mother cell. Outer spindle is seen in transverse position. × 840.

Fig. 8. Four megaspores, two of which are lying in the longitudinal, the other two in the transverse axis of the nucellus. × 840.

Fig. 9. Four megaspores, the two outer lying over each other giving the appearance of only three being present. The fourth nucleus is faintly visible. × 840.

Fig. 10. Four megaspores in a nearly straight row. × 840.

Fig. 11. Germination of megaspores. Nuclei of the two inner megaspores dividing. × 720.

Fig. 12. Eight-celled stage of the embryo-sac showing four nuclei at either end and the remnants of megaspore nuclei at the micropylar end. × 840.

Fig. 13. Embryo-sac showing antipodal cell, definitive nucleus, egg apparatus and remains of megaspore nuclei. × 620.

Fig. 14. Two-celled embryo, endosperm nuclei and three antipodal cells. × 620.

Fig. 15. Young embryo consisting of three cells. Two endosperm nuclei dividing. × 630.

Fig. 16. Free cell formation in early stages of endosperm development. Antipodal cells becoming prominent. × 420.

Fig. 17. Polar nuclei approaching and meeting near the middle of the sac. × 720.

Fig. 18. Three much enlarged antipodal cells. × 720.

Fig. 19. Suspensor in contact with endosperm. × 720.

Fig. 20. Development of endosperm tissue, appearance of walls after a period of free cell formation. × 720.

Fig. 21. Young embryo and surrounding endosperm. Antipodal tissue invading the latter. × 325.

Fig. 22. Section through ripe ovule showing integuments. × 82.

Fig. 23. Antipodal tissue with large nuclei and darkly staining bodies in the cytoplasm. × 390.

Fig. 24. Massive suspensor, embryo removed from endosperm. × 720.

Fig. 25. Embryo with groove in which leaves and plumule appear. × 107.

Fig. 26. Embryo after groove has closed up and suspensor has been obliterated. (Drawn from reconstructed model.)

Fig. 27. Club-shaped embryo and surrounding endosperm. × 630.

Fig. 28. Section through ripe fruit showing naked embryos in place.

Fig. 29. Section through embryo showing suspensor and groove in which the plumule and leaves are to develop. × 107.

Fig. 30. Archesporial cell, with "tapetal" cell just cut off. × 500.

Fig. 31. "Tapetum" dividing by an anticlinal wall. × 500.

Fig. 32. Late stage in the division of the spore-mother cell, spindle still visible. × 500.

Fig. 33. Pollen tube entering ovule through the micropyle. × 220.

Fig. 34. First division of the spore-mother cell completed. "Tapetum" clearly shown. × 500.

Fig. 35. Embryo with surrounding endosperm. Nucellar tissue nearly destroyed, inner integument breaking down. × 43.

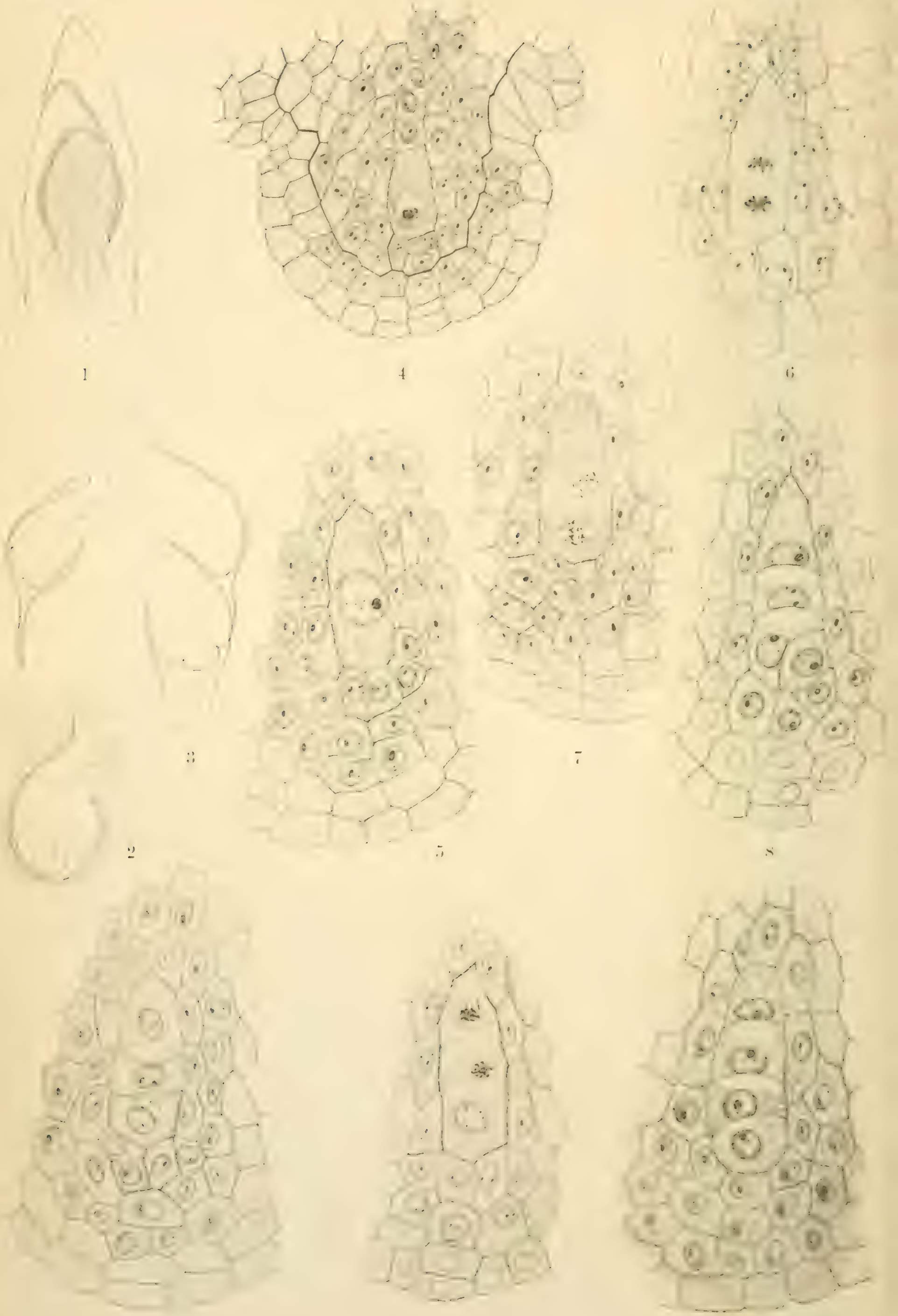
Fig. 36. A more advanced stage than the preceding. Antipodal tissue with large deeply staining nuclei. × 43.

Fig. 37. Young club-shaped embyro with surrounding endosperm. × 203.

Fig. 38. Pear-shaped embryo with short suspensor. × 70.

Fig. 39. Section through the suspensor end of the embyro showing groove and in it the rudiments of leaf and plumule. × 150.

Fig. 40. Section through mature embyro showing the radicle and vascular bundle leading off into the "cotyledon." Two leaf rudiments and stem apex are faintly visible. × 38.



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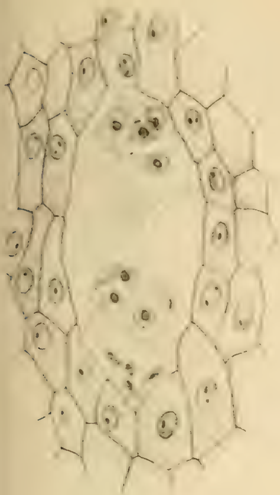
PLAT



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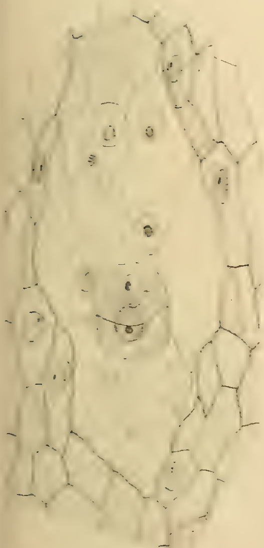

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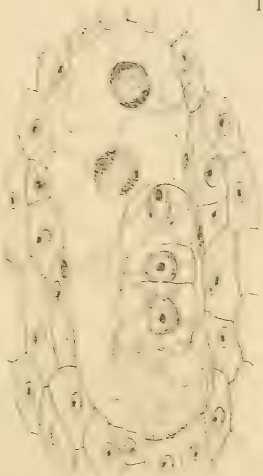

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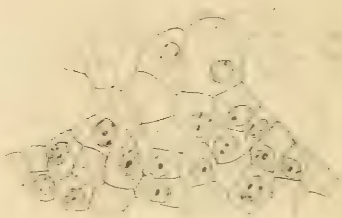

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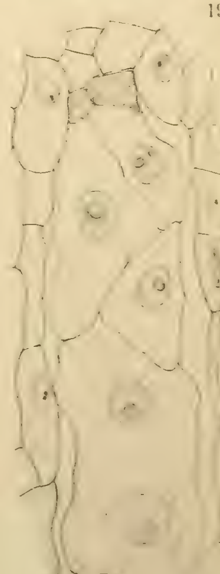

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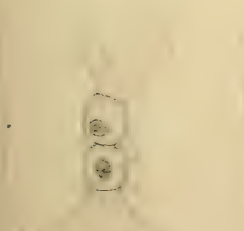

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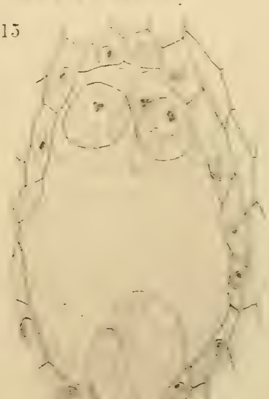

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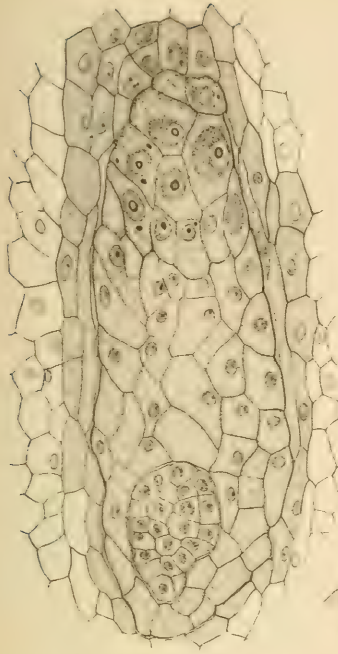

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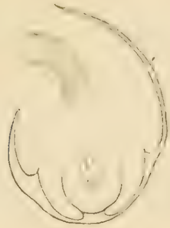

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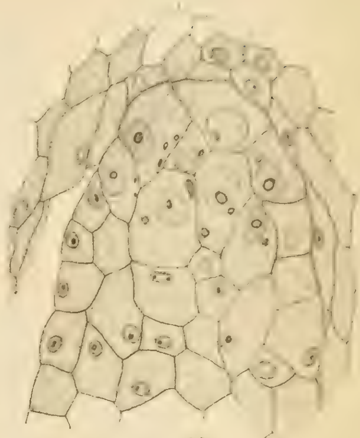

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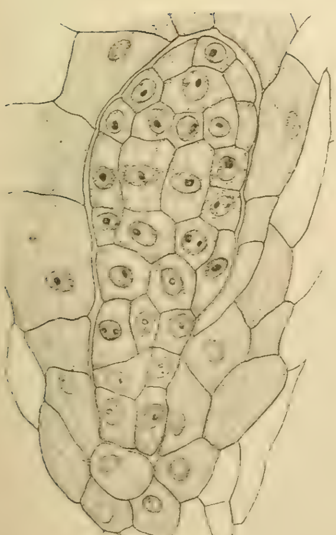

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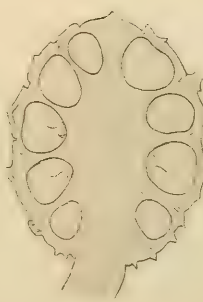

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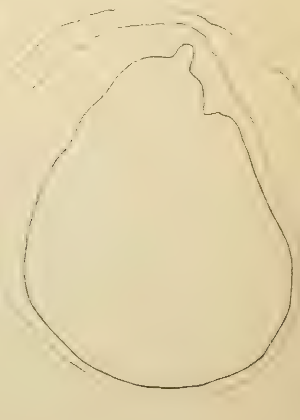

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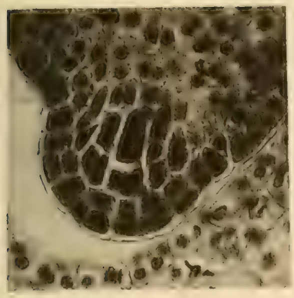
PLATE II.

HELIOTYPE CO., BOSTON.



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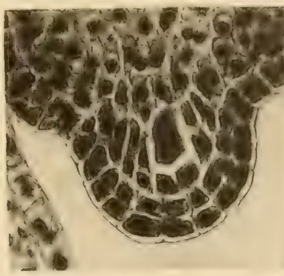

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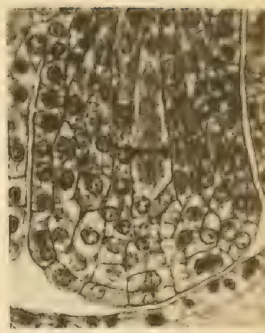

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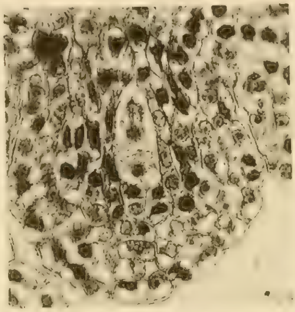

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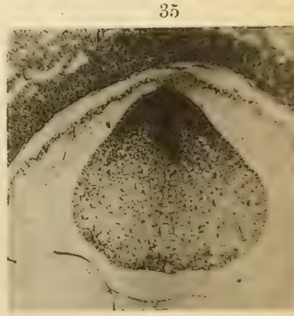

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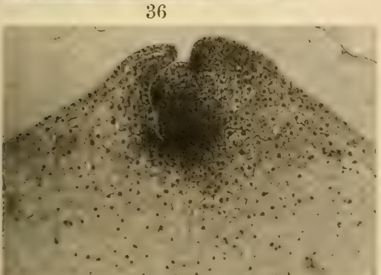

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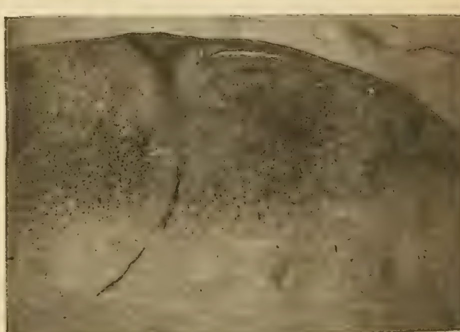

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C. O. R. Photo.

PLATE III.

HELIOTYPE CO., BOSTON.

2. THE SEEDS AND SEEDLING OF CAULOPHYLLUM THALICTROIDES.

Frederic K. Butters.

Caulophyllum thalictroides (L) Michx. is fairly abundant throughout the whole northeastern part of the United States, and also occurs in eastern Asia. Although it has been known to botanists for almost two centuries very little work has been done on the structure and development of the seed, and the germination of the seed appears never to have been observed.

Dr. Asa Gray[1] described and figured the developing fruit, and the structure of the mature seed. In 1904 Mr. Charles E. Lewis[2] published a short account of the later stages in the development of the embryo in connection with work on the embryogeny of several closely related plants. He appears to have been in error in several of his conclusions concerning *Caulophyllum* as will appear in the course of this article.

The material used in investigating the development of the ovules and seeds was obtained in the vicinity of Minneapolis where the plant is very abundant. It was killed in the field in chrom-acetic acid, handled and cut in the usual way, and stained either with iron-alum-haematoxglin, or with the triple safranin-gentian-violet-orange G. stain. Ripe seeds were germinated in the plant house and the seedlings from these were compared with others collected in the field.

The writer wishes to express his thanks to Dr. H. L. Lyon for aid in collecting material, and for many valuable suggestions made during the early part of this investigation.

The Fruit.

As is well known, the fruit of *Caulophyllum* consists of a pair of stalked, drupe-like seeds subtended by a small scale, the almost ves-

[1] The Genera of the Plants of the United States, 1 : 81, 1849.

[2] Studies on Some Anomalous Dicotyledonous Plants. Bot. Gaz. 37 : 127, 1904.

tigial pericarp. The gynaeceum of the flower consists of a single carpel enclosing two large, erect, anatropous ovules. These stand side by side in the ovary, with their micropyles turned away from each other. Even in the bud the edges of the carpel are in loose contact, and the cavity of the ovary is in communication with the exterior by a very narrow slit which opens upon the stigmatic surface of the pistil. After flowering the carpel undergoes very little growth. In less than two weeks the developing seeds push it open, and are entirely exposed, the carpel remaining as a small bract-like structure at the base of the seeds.

Development of the Ovule.

The ovule shows no marked peculiarities in its development. It has from the beginning a long and massive stalk (150 mic. x 180 mic.). The nucellus is formed at the distal end of this. In the youngest ovules sectioned (about a month before the opening of the flowers) the nucellus appears as an almost hemispherical mound of tissue directed obliquely upwards at the distal end of the ovule. At this stage the primordium of the inner integument appears as a collar-like ridge encircling the nucellus, and scarcely protruding above the general surface of the ovule, while the only trace of the primordium of the outer integument is a slight convexity of the tissues at the distal end of the ovule opposite to the nucellus (Text figure 1, A). The nucellar mound grows rapidly in height becoming first hemispherical and then elliptical in outline. At the same time the unequal growth of the distal portion of the stalk causes the axis to bend rapidly, turning the nucellus into first a lateral and finally an inverted position. During this bending of the axis, the outer integument appears first as an outgrowth from the summit of the bending stalk, and then, as it develops farther down the sides of the stalk, as a hood-like covering about the nucellus. From the beginning it is much more massive than the inner integument, and when it has once begun to develop it grows more rapidly than the latter.

About twenty days before flowering (Fig. 1, Pl. IV), both integuments are about one-half the length of the nucellus. The inner integument is two or three cells in thickness, the outer, about twice as thick. Thereafter the outer integument is the longer. It completely covers the nucellus at least ten days before the flowers open, while the inner integument closes over the top of the nucellus sev-

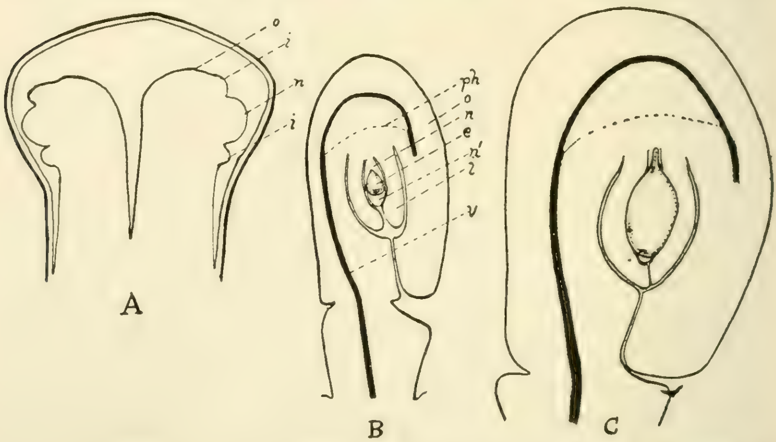
eral days later. Both integuments increase considerably in thickness as a result of tangential cell division, so that in the ovules of open flowers the outer integument is 200-300 mic. in thickness, and the inner integument from one-fourth to one-third, as thick. Considerable specialization of the cells of the integuments occurs before the flowers open. The inner layer of cells of the inner integument undergo frequent radial divisions. At the same time their protoplasm becomes more dense, so that they come to form a very distinct layer of columnar cells next to the remains of the nucellus, and to such parts of the embryo-sac as are no longer covered by the nucellus. A somewhat similar modification occurs in the inner layer of cells of the outer integument, but the specialization of this layer never becomes so well marked as in the case of the inner integument. During the same period the stalk of the ovule increases considerably in thickness, and a marked constriction is developed between the stalk and the body of the ovule.

The earlier stages in the development of the embryo-sac cannot all be traced in the material at hand. Sections taken about twenty days before flowering show a cell about 20 mic. x 32 mic.—larger than the adjacent nucellar cells, and with more vacuolar protoplasm. The nucleus is in synapsis, and the cell is apparently the megaspore-mother cell (Fig. 1, Pl. IV). The young embryo-sac increases rapidly in length, and the micropylar end increases also in width, while the antipodal end becomes attenuated. Thus about ten days before flowering the embryo-sac is a club-shaped structure, about 120 mic. long, 60 mic. wide at the micropylar end but with the antipodal one-third only 8 mic. wide. At this stage the embryo-sac commonly shows two or four nuclei, the antipodal nuclei being located at the entrance to its narrow, antipodal portion.

The growth of the embryo-sac is not associated with a corresponding growth of the nucellus. The cells of the nucellus next to the embryo-sac break down as the latter structure grows, and the outer cells are pushed apart so that the distal end comes to form a cap-like structure at the micropylar end of the embryo-sac (*n′* Fig. 2, Pl. IV). This structure persists until the seeds are almost mature. A few cells at the proximal end of the nucellus remain as a sheath about the narrow antipodal end of the embryo-sac (*n* Fig. 2, Pl. IV). Between these portions of the nucellus the embryo-sac comes into direct contact with the inner integument.

THE MATURE OVULE.

At the time of flowering the ovule is about 1 mm. long by .6 mm. wide (exclusive of the stalk, which is about .3 mm. long by .4 mm. wide). It has a somewhat rectangular oval outline. The nucellus and the integuments are united in a broad and massive chalazal region. A strand of vascular tissue extends up from the stalk. On reaching the chalazal region this divides, and the xylem passes over and around the chalazal region in two strands, while the phloem spreads out laterally in a hood-like form and almost completely covers the chalazal end of the ovule. (Text Fig. 1, B & C). The cells which lie between the vascular strands and the antipodal end of the embryo-sac increase considerably in size, averaging about twice as large as the other parenchyma cells of the integuments,



Text Figure 1. Development of the ovule. A. Ovules in ovary five weeks before flowering. × 100. B. Ovule ten days before flowering. × 40. C. Ovule at flowering time. × 40. *o*, outer integument, *i*, inner integument, *n*, *n'*, nucellus, *e*, embryo-sac, *v*, vascular bundle, *ph*, phloem, spreading out from bundle in chalazal region of ovule. The xylem strand is double in this region.

and become somewhat vesicular. This group of cells later gives place to the peculiar cavity found in the chalazal region of the maturing seeds.

The cavity of the outer integument is oval with the narrow end towards the micropyle. The outer part of the latter structure is a tubular canal 4 mic. in diameter and about 300 mic. long, the inner

part is somewhat narrower and about 120 mic. long. The external opening of the micropyle is situated at the bottom of the groove which separates the stalk from the body of the ovule, the internal opening is behind the nucellar cap.

The embryo-sac is clavate, about 340 mic. long, 20 mic. in diameter at the antipodal end, and 130 mic. at its widest portion. The wide part of the embryo-sac has a very thin parietal layer of protoplasm surrounding a large vacuole. At the micropylar end the egg apparatus forms a nearly spherical mass about 40 mic. in diameter which projects strongly into this vacuole. The egg nucleus lies near the inner end of this mass and is about 8 mic. x 16 mic. The synergids lie at one side of the egg nucleus, and nearer the wall of the embryo-sac. Their nuclei are very small, and their cytoplasm is vacuolate, and is sharply distinct from the protoplasm of this embryo-sac. The small antipodal portion of the embryo-sac is filled with cytoplasm and contains the antipodal nuclei which are small and appear to be on the point of breaking down. The primary endosperm nucleus is large, and is located near the micropylar end of the embryo-sac.

Fertilization was not observed although in several preparations remains of the pollen-tube were seen within the micropyle. The pollen-tube apparently enters the embryo-sac between the inner integument and the nucellar cap.

Development of the Seed after Flowering—The Integuments.

The outer integument increases greatly in thickness, especially in the chalazal region. The superficial cells of this integument become specialized, their contents become somewhat denser, their outer walls become thickened and a distinct cuticular layer is formed. The cells of this epidermis undergo many anticlinal divisions as the seed matures. In surface view they present somewhat irregular outlines, and heavy vertical walls. This layer of cells forms the firm and waxy covering of the ripe seed.

About a month after flowering, the form of the embryo-sac begins to undergo a marked change due to the peculiar development of the outer integument in the vicinity of the micropyle. The integument grows very rapidly in a ring-like area surrounding the micropyle. The end of the embryo-sac becomes first flattened, and then invaginated. This ingrowth of the integument increases until, in the mature seed, it extends about one-third of the distance across

the embryo-sac. The tissues immediately adjacent to the micropyle do not grow so rapidly as those somewhat more remote, and so the inner opening of the micropyle comes to occupy the bottom of a narrow, cup-like depression in the top of the ingrowth just described. This depression is filled, in the mature seed, with endosperm, and in this portion of the seed the embryo develops. (Text figure 2). The ingrowth of the outer integument is accomplished almost wholly by a great increase in the size of the interior cells of the region, which increase from an average size of 40 mic. x 48 mic. to one of 60 mic. x 190 mic., the longest dimension lying parallel to the micropylar canal. There is comparatively little cell division except in the inner layer of the integument where cell division is for a time quite active.

In the ripe seed, the whole outer integument except the epidermis becomes fleshy, the invaginated portion being more dry and spongy than the outer parts. No structure derived from either integument becomes firm and hard in the mature seed, the hard part of which is composed entirely of endosperm.

The inner integument is at its maximum development in thickness at, or soon after, the flowering period. Its inner columnar layer maintains its character for some time by frequent vertical cell divisions, but finally its cells become stretched and much flattened by the rapidly growing embryo-sac. The cells in the layer directly outside of the columnar layer begin to break down and collapse within ten days of the flowering period. This change gradually involves the outer layers, until in full grown seeds the inner integument consists of little but the much flattened cells of the once columnar layer, backed by a broken down and collapsed mass of cells, or at most by a single layer of much flattened living cells.

These changes are most marked in the middle portions of the ovule, where growth is most rapid. In the immediate vicinity of the micropyle, and also in the antipodal region the inner integument retains permanently very much the same structure which it has throughout, at the time of flowering.

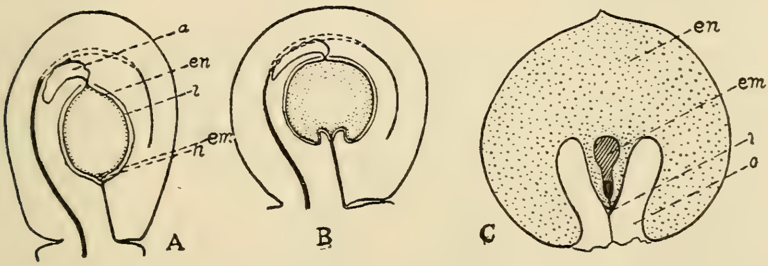
Endosperm.

The primary endosperm nucleus divides even before the perianth of the flower falls, and further divisions follow rapidly, the nuclei passing around in the thin parietal layer of cytoplasm so that they

become somewhat uniformly scattered throughout, with a group of several near the antipodal end of the embryo-sac (Fig. 2, Pl. IV). For some time, at least, the divisions of all the endosperm nuclei are simultaneous.

Until the seeds are one-half their ultimate size—about one month after flowering—the endosperm remains as a parietal layer not over 25 mic. thick surrounding the large central vacuole of the embryo-sac, and containing rather numerous large nuclei (8 mic. x 16 mic.). These nuclei are somewhat flattened in form, and lie in a single layer, without any intervening cell walls.

About four weeks after flowering, the endosperm layer begins to thicken, and anticlinal cell walls appear between the nuclei. As the cytoplasm thickens, some of the nuclei migrate in towards the center of the embryo-sac, and the development of cell walls proceeds centripetally. In this manner in less than ten days, the whole cavity of the seed becomes filled with parenchymatous endosperm.



Text Figure 2. Development of seed. A. Ten days after flowering. × 10. B. Six weeks after flowering. × 5. C. Ripe seed with the fleshy testa removed except the invaginated portion. × 5. *En*, endosperm, *em*, embryo, *a*, chalazal vesicle, other letters as in text fig 1.

This period coincides in time with the invagination of the micropylar end of the embryo-sac, and is the period of most rapid growth in the seed.

For some time after the endosperm becomes cellular, growth continues throughout, with frequent cell divisions, and the tissue remains very thin-walled. Finally, when the seed is almost ripe, the walls become much thickened, and in the dry, ripe seed the endosperm is exceedingly hard. It contains no starch at any time, the reserve materials of the seed being stored in the form of oil, and of the thick cellulose walls of the endosperm cells.

Chalazal Vesicle.

After the flowering period the antipodal end of the embryo-sac increases but little in size, but cells of the lower part of this region become vesicular, and grow down into the adjacent chalazal region, breaking down the large cells which lie between the embryo-sac and the vascular tissue of the ovule. A large cavity is thus formed in the chalazal region of the ovule which is lined by a very thin layer of protoplasm containing a few very large nuclei (Text figure 2, A and B). This cavity is cut off from the cavity of the embryo-sac by thin cell walls across the narrow part of the embryo-sac (Fig. 10, Pl. IV).

The origin of the invading cells could not be determined with entire certainty, but it appears most probable that they are specialized endosperm cells which become cut off from the main body of the endosperm very shortly after flowering. In sections taken at flowering time the antipodal nuclei are seen as small darkly staining bodies which appear to be in rapid degeneration. In preparations made a little later in which the endosperm is actively developing, three to five very large nuclei are seen occupying the narrow part of the embryo-sac. They closely resemble the ordinary endosperm nuclei, and it seems much more likely that this is their character than that the antipodal cells, already in an apparently degenerate conditions should suddenly become active again. The protoplasm surrounding these nuclei becomes cut off into distinct cells long before any general cell formation takes place in the endosperm, and it is the growth of these cells down into the chalazal tissues which results in the vesicular cavity just described.

This structure undoubtedly serves to put the embryo-sac into closer communication with the vascular tissue of the ovule, and appears to continue functional throughout the ripening of the seed.

The Embryo.

After fecundation the oosperm forms a thin cell wall about itself. The cell thus formed is at the extreme micropylar end of the embryo-sac abutting on the cap-like remains of nucellus (Fig. 2, Pl. IV). It is covered with a thin layer of cytoplasm belonging to the endosperm, while the degenerate remains of the synergids can sometimes be distinguished at one side of it, close to the base. The oosperm cell which is at first almost spherical, increases gradually

in length until it is about 35 mic. long. Its cytoplasm becomes considerably vacuolate particularly in the lower part. The nucleus is situated above the center of the cell and is of moderate size (about 12 mic. in diameter), densely granular, and with a distinct nucleolus.

The first cell division in the embryo occurs from two to three weeks after flowering (Figs. 3 and 4, Pl. IV). It is transverse, and divides the embryo into dissimilar cells. The lower, or suspensor cell is larger than the upper cell and has vacuolate cytoplasm. The nucleus is usually situated in the upper part of this cell, and decreases in size as the growth of the embryo goes on. The upper cell has denser cytoplasm, and usually a larger nucleus than the suspensor cell. The succeeding cell divisions seem to be quite irregular (Fig. 5-9, Pl. IV). The primary suspensor cell usually remains undivided, but it may divide in a plane perpendicular, or somewhat oblique to the first division (Fig. 9, Pl. IV).

The upper of the two cells formed by the first division sometimes divides in a plane perpendicular to the first division. In other cases this second division plane appears to be oblique to the first, and cutting it at a more or less acute angle, while in a few cases the arrangement of cells in a slightly older embryo indicates that the upper cell divided transversely in a plane almost parallel to that of the first division. Subsequent cell divisions are oblique, and there is thus built up an oval or almost spherical embryo of which the suspensor cell or cells (when the primary suspensor cell has divided) form at first about one-third (Fig. 11, Pl. IV). The cells adjacent to the primary suspensor cell gradually take on the cytological characters of that cell, though they generally remain considerably smaller than it. Their protoplasm becomes vacuolate, and contains numerous highly refractive granules, their nuclei decrease in size and stain more heavily.

The cells in the distal portion of the embryo continue to divide in all directions, and thus is gradually built up a pear shaped embryo with a massive but somewhat slender suspensor (Fig. 12, Pl. V).

The development of the embryo is slow, so that a month after the flowering period, at a time when the seed is three-fourths of its mature size, and the endosperm is developing rapidly, the embryo has reached a length of only 150 mic.,—less than one-twelfth of the length of the embryo of the mature seed. It will be recalled that at about this time the change takes place in the shape of the microp-

ylar end of the embryo-sac. As a result of this change the embryo comes to occupy the bottom of the cup-like depression which forms the middle of the invaginated part of the seed. The growth of the embryo continues with little change of form until it is about 500 mic. long, and 200 mic. in diameter at the widest part. At about this time growth in length in the distal part of the embryo becomes confined largely to the peripheral region, while growth in thickness continues throughout. The result is that the distal end of the embryo becomes flattened and apparently in some cases even slightly concave. At about this stage the primordia of the cotyledons appear, as two mound-like outgrowths occupying opposite sides of the margin of the distal end of the embryo. They grow rapidly in length, while the margin of the embryo between them grows little or none. The morphological apex of the embryo which eventually gives rise to the growing point of the stem is at this stage very little or not at all prominent. The shape of the embryo at the time of the appearance of the cotyledons is usually nearly or quite symmetrical, but a slight asymmetry occurs in some cases, one side of the embryo being very slightly higher and more prominent than the other, or the cotyledonary mounds developing at points, not quite diametrically opposite. This asymmetry when present appears to affect the pear-shaped embryo quite independently of the orientation of the cotyledons. In no case do the cotyledons appear to arise first as a single crescentic ridge, but always as distinct mound-like outgrowths which are usually very symmetrically placed on opposite sides of the distal end of the pear-shaped embryo (Pl. X; Fig. 12, Pl. V).

The cotyledonary mounds grow rapidly into somewhat broad, thick, blunt, and usually very symmetrical cotyledons. While it appears possible that the sinus between the cotyledons may be sometimes a little deeper on one side than on the other owing to the possible slight asymmetry of the embryo, yet this is certainly not the rule, and it is probable that in almost all cases in which the transverse sections seem to indicate this peculiarity, the appearance is due to slightly oblique sectioning.[1]

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[1] This conclusion is diametrically opposed to that reached by Mr. C. E. Lewis (Studies on some Anomalous Dicotyledonous Plants, Bot. Gaz. 37: 127, 1904.) In studying the origin of the cotyledons sections were made of a large number of embryos in which the cotyledonary primordia were 20 mic.—40 mic. in height (the cells of this part of the embryo are about 20 mic. in diameter)

After the cotyledons appear they grow much faster than the body of the embryo, so that about ten days after the first appearance of their primordia the cotyledons equal the hypocotyl in length, the embryo exclusive of the suspensor measuring about 1 mm. in length.

Later, the growth is much slower, the embryo reaching the length of 1.5 mm.-1.7 mm. during the succeeding month, and 2 mm.-2.25 mm. in the ripe seeds collected in autumn. Of this length about three-fifths is occupied by the cotyledons (Fig. 15-17, Pl. V).

There is no tendency to develop a cotyledonary tube during the maturing of the embryo as is the case in Podophyllum and some other related plants, but the cotyledons remain separate, the sinus on each side extending to their base (Fig. 16, Pl. V). The growth of the cotyledons is accomplished by cell division occurring throughout their tissue. At first they increase somewhat in thickness as well as in length in their proximal portion, but not at the extreme base, nor in the distal half. The latter part grows considerably in width. The result is that the cotyledons become somewhat spoon-shaped with the concave faces toward each other. They are contracted at the base, while immediately above this they approach each other, almost enclosing a small conical space above the apical portion of the axis of the embryo (Fig. 15, Pl. V). This apical growing region of the epicotyl at first projects little above the plane of the bases of the cotyledons, but it gradually develops, and in the mature seed forms an epicotyledonary mound of tissue about 80 mic. high, which nearly fills the conical space between the bases of the cotyledons. As the embryo grows it disorganizes the surround-

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and wax models were reconstructed from the sections in the case of several embryos, series both of longitudinal and of transverse sections being thus employed. In reconstructing embryos of *Caulophyllum* the remarkably symmetrical shape of the part of the seed in which the embryo is located is of great aid in determining in what degree the sections are oblique to the axis of the seed. This angle was carefully calculated for each series of sections previous to reconstruction. Although in several series sections occurred almost exactly like those figured by Mr. Lewis, their peculiar shape proved to be due to oblique sectioning of the embryo, and not to the crescentic primordium which Lewis postulates.

Subsequent to the reconstruction of the embryos shown in Plate X, a number of embryos were dissected out of seeds and examined directly under a Zeiss binocular dissecting microscope. They were found to have almost exactly the form which had been obtained by reconstruction and which is shown in Plate X. There is in fact, less, rather than more, deviation from perfect symmetry than is shown by the models.

ing endosperm tissue, and is surrounded by a layer of disorganized cells 120 mic.-500 mic. in thickness. A portion of this broken-down endosperm becomes enclosed by the cotyledons and is to be seen even in the mature seed as a small mass of structureless material between their bases.

Differentation of Tissue in the Embryo.

During the early stages of its development, up to the period when the cotyledons appear, the only differentiation in the tissues of the embryo is that previously noted by which first the basal cell or cells and progressively those above this lose the power of further division, and become somewhat vesicular, forming the suspensor. The body of the embryo throughout this stage of development consists of an entirely undifferentiated mass of cells with dense granular protoplasm and large nuclei. Cell division occurs abundantly throughout this mass of tissue, and apparently in no regular order or direction. Spindles may frequently be found close together and running at various angles to one another. There is not even a differentiated epidermis and while most of the cell division in the superficial cells is radial, tangential divisions have been observed in these cells in embryos over 300 mic. in length, and are plainly indicated in yet older ones.

About the time that the cotyledons begin to develop, the first signs of tissue differentiation appear. This seems to be brought about by a specialization in the direction of cell division in the various parts of the embryo. In the axial region the cells divide both transversely and longitudinally, the latter direction predominating, while the cell division is accompanied with comparatively little cell growth, the peripheral cells divide mainly transversely, and undergo considerable cell growth. This results in the formation of a plerome strand of comparatively small, cylindrical and irregularly arranged cells surrounded by a periblem region of larger and less cylindrical cells which are arranged in somewhat irregular longitudinal rows. These rows curve inward at the suspensor end of the embryo, and appear to radiate from a region in the axis of the embryo just above the suspensor, which becomes the growing point of the root (Fig. 15, Pl. V). Apparently this growing point functions somewhat during the further development of the embryo, but growth is not localized there, and cell divisions are scarcely more numerous there than elsewhere.

The plerome and periblem regions thus differentiated are not sharply distinguished from each other. Although each region is characterized by certain peculiarities of cell behavior, these peculiarities are not absolutely fixed, and there is never a sharp line of demarcation between the two regions.

Even in ripe seeds there is scarcely any differentiation between the cells of the plerome, the characteristic differences between xylem and phloem appearing after growth is resumed.

As the cotyledons develop, plerome strands become differentiated in them in a manner similar to the formation of plerome in the axis. There are three of these strands in the lower part of each cotyledon. They branch, and become more numerous in the broad upper portion of the cotyledon, while at the base they fuse into the general plerome cylinder of the axis.

The epidermis becomes very slowly differentiated, and is for the most part but slightly specialized even in the ripe seeds. Its cells are somewhat smaller than the underlying periblem cells, and their protoplasm is more dense. The epidermis becomes most highly specialized in the upper parts of the cotyledons. On the inner surface of their concave distal parts several stomata are developed (Fig. 17, Pl. V). These have the usual form of such structures. Their presence is especially interesting in view of the fact that the cotyledons never become epigean.

The cells immediately below the growing point of the root, and next to the suspensor divide several times transversely, forming the primordium of the root cap (Fig. 12, Pl. V et seq.). The development of this structure extends laterally about the convex end of the periblem, the cell divisions being always parallel to the surface of the latter tissue, and finally it extends across the whole width of the embryo, involving tangential divisions of the epidermal cells where it comes out to the surface of the embryo. During its further development the root cap thickens considerably, especially in the axis of the embryo where it is ten to twelve cells thick in the ripe seed.

The cells at the distal end of the axis of the embryo, which eventually give rise to the growing point of the stem, change very little during the maturing of the seed. In the ripe seeds they appear as a low mound of irregularly arranged isodiametrical cells covered by a fairly distinct epidermis (*e*, Figs. 15 and 16, Pl. V).

Germination of the Seed.

The seeds of *Caulophyllum* germinate very slowly. Seeds were collected and planted in the autumn, before the pulp had dried, and others were planted in the spring after lying under the snow for one winter. None of them showed any external signs of germination in the following December—fifteen months after their maturity. An examination of the embryo of these seeds (Fig. 18, Pl. V) showed, however, that it had increased considerably in size. The cotyledons, especially, were found to have elongated to over twice their former length, and to have increased by one-half in width, and they had pushed their distal ends well up into the body of the seed. Although the hypocotyl had increased somewhat in length, changes in that region were far less marked than in the cotyledons. The epicotyl was almost unchanged except for a slight growth most noticeable from the development of definite rows of cells in the interior where the cells were irregularly parenchymatous before.

After this stage is reached, the germination of the seed progresses rapidly, if the environment is favorable. This occurs usually, under natural conditions, during the early part of the second summer. The radicle projects from the seed, partly as a result of its own growth, partly on account of the rapid elongation of the proximal portion or petioles of the cotyledons. This process continues until the entire hypocotyl is pushed out of the seed with which it is connected by the two cotyledonary petioles about 8mm. long. At the same time the spoon-shaped distal portions of the two cotyledons grow rapidly, coalesce, and together form a peculiar haustorial organ which occupies the center of the seed. This haustorium takes the form of a hollow sphere invaginated on one side, thus conforming in a general way to the shape of the seed (Figs. 21 and 22, Pl. VI). Its wall is about one-half mm. thick, and its surface is marked with low convolutions. While the line which marks the division between the two cotyledons in this haustorium can be seen on close examination, it is not at all conspicuous, and the union of this portion of the cotyledons appears to be complete. As the petioles of the cotyledons elongate, they form a very short cotyledonary tube (about 100 mic. long) at their base. Otherwise they are entirely separate. They join the haustorium at the middle of its concave side. During the first year's extra-seminal growth of the embryo, the haustorium continually increases in size, until at the close of the

season it has completely absorbed the endosperm. It then withers away together with the petioles of the cotyledons, and no trace of the seed is to be found at the beginning of the next season (Pl. VII).

Fed by the large amount of nutriment absorbed from the endosperm by the haustorium, the hypocotyl rapidly elongates and gives rise to the rather stout primary root (Pl. VI). This grows downward in a somewhat irregular course, and by the end of the season has usually a length of about 12 cm. Its diameter is 1.0-1.5 mm. By the time the primary root is 8 cm. long, lateral roots begin to grow out from it, the first appearing about 1 cm. below the attachment of the cotyledons, and later others farther down. These lateral roots have about one-half the diameter of the primary root. By the end of the season several of them may attain a length of over 2 cm.

In contrast to this rapid development of an efficient root system, the epicotyl grows very slowly. During the first season the stem axis elongates very little, and usually no foliage leaves are produced, but only about five scale-leaves which grow up over the tip of the axis forming one of the typical winter buds of the plant. Within this bud are produced the primordia of the foliage leaves of the next season's growth, and in the axils of the cotyledons, and of the bud scales may already be distinguished the primordia of the first lateral branches of the stem. It is thus seen that the first season's extra-seminal growth of the seedling may be entirely hypogean, and it seems probable that under natural conditions it is always so. Of seedlings started in the hot-house during the winter a very few (less than 10 per cent. of the total number) produced a small foliage leaf during the latter part of the following summer. In these cases the foliage leaf took the place of the first of the bud scales which are usually produced, and a very small winter bud was formed at its base (Fig. 23, Pl. VI).

Later Development of Seedling.

The second year's extra-seminal growth (Pl. VII) does not differ essentially from that during the several following years. A foliage leaf appears above ground in the early spring, and a few weeks later it is followed by another. They persist throughout the summer. Above these several scale leaves are produced which form the scales of the next winter bud. The foliage leaves for several seasons are usually simply trifoliolate.

For several years all the internodes are very short and the stem axis elongates very slowly (about 4 mm. per year). Its growth is at first upward, but gradually changes into the horizontal growth of the mature rhizome. If the terminal bud is uninjured the main stem does not send out any lateral branches for several years, and the lateral buds which are formed each year remain dormant. Some of them finally grow, producing the characteristic branched rhizome of the mature plant. An injury to the terminal bud will at any time start one of the lateral buds to growth to take the place of the injured terminal.

The primary root system enlarges for several years. Secondary roots begin to grow out from the older parts of the rhizome after four to ten years' growth, the time depending apparently on the luxuriance of the plant (Pl. IX). Several years later the primary root withers and disappears, and thereafter a certain amount of the older part of the rhizome with the attached roots dies each year. Finally when flowering stalks appear (in nature apparently only in very old and well established plants) the stem axis abandons its simple monopodial system of growth, and each year the main axis develops into the subaerial leafy flower-bearing shoot, and the additional growth of the rhizome for the season occurs as a lateral branch from the axil of one of the scale-leaves of the winter bud.

The Vascular Skeleton of the Seedling.

Definite differentiation of the vascular tissues of the embryo occurs early in the process of germination. The formation of phloem and protoxylem occurs first in the middle bundles of the cotyledons, and shortly afterwards in the lateral bundles. It is well advanced in the lower half of the cotyledons before any differentiation of tissues can be made out in the plerome of the hypocotyl. At the same time the epicotyl still consists of an undifferentiated mound of meristem cells (Fig. 18, Pl. V). The differentiation of the vascular tissues extends upward into the upper part of the cotyledons, and downward into the hypocotyl.

Primary Structure of the Hypocotyl.

The very slow development of the epicotyl together with the strong development of the cotyledons and roots, and the compara-

tively great length of the hypocotyl render the seedling of *Caulophyllum* a very favorable object for the study of this interesting region.

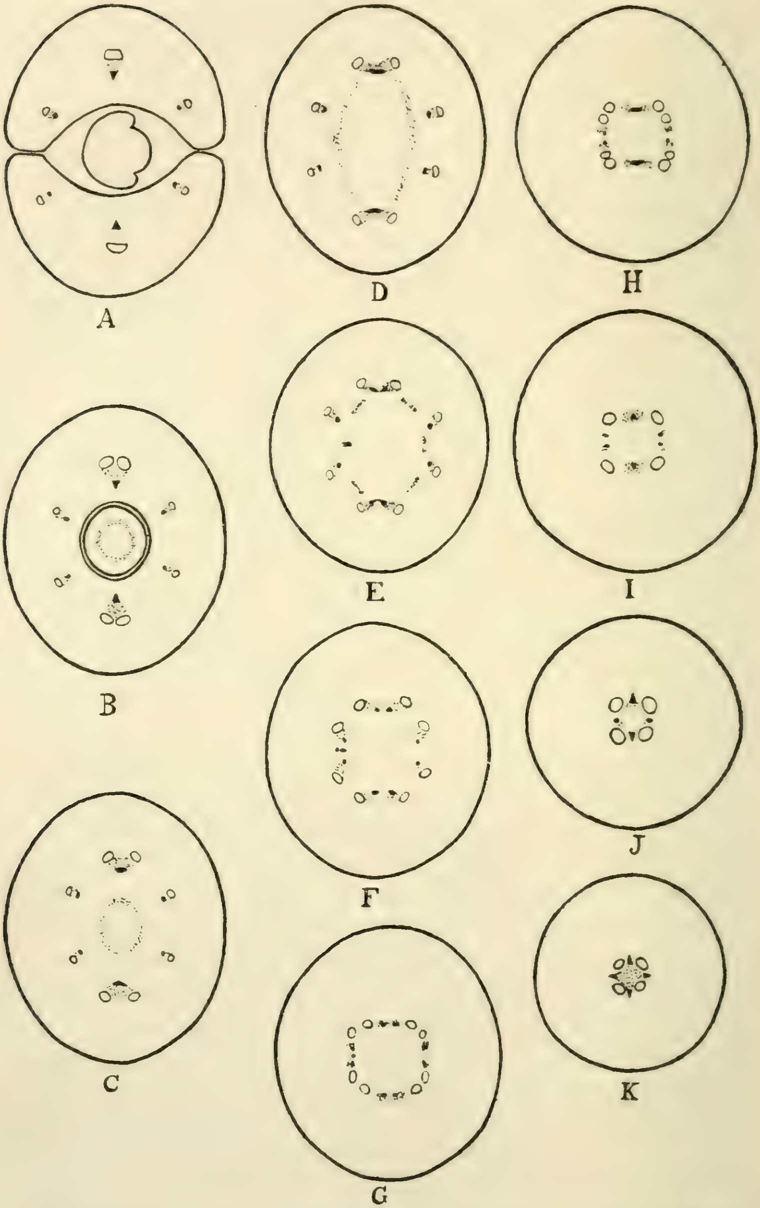
From each cotyledon three distinct vascular bundles enter the hypocotyl. These all have the structure and orientation of ordinary stem bundles. The median bundle from each cotyledon is somewhat larger than the lateral ones (Text Fig. 3, a). Shortly after entering the hypocotyl these larger bundles show a double structure in the phloem region and the two phloem groups of each bundle gradually diverge (Text Fig. 3, b, c, d), the as yet undifferentiated central part of the bundle also divides, and finally the protoxylem divides also. Below this there are for some distance eight distinct cotyledonary bundles in the hypocotyl (e, f, g).

The bundles gradually twist so that the phloem group of each lateral bundle is approximated to the phloem group of the corresponding median bundle. A little lower, the phloem groups separate from the xylem (g) and at about the same level the xylem groups originating from each of the median bundles approach each other and reunite, forming first a band of xylem with protoxylem in the middle and metaxylem at each end, and along the outside of the band (h). A little lower the protoxylem concentrates into a single small mass and the metaxylem passes into the centripetal position which is characteristic of root steles (i).

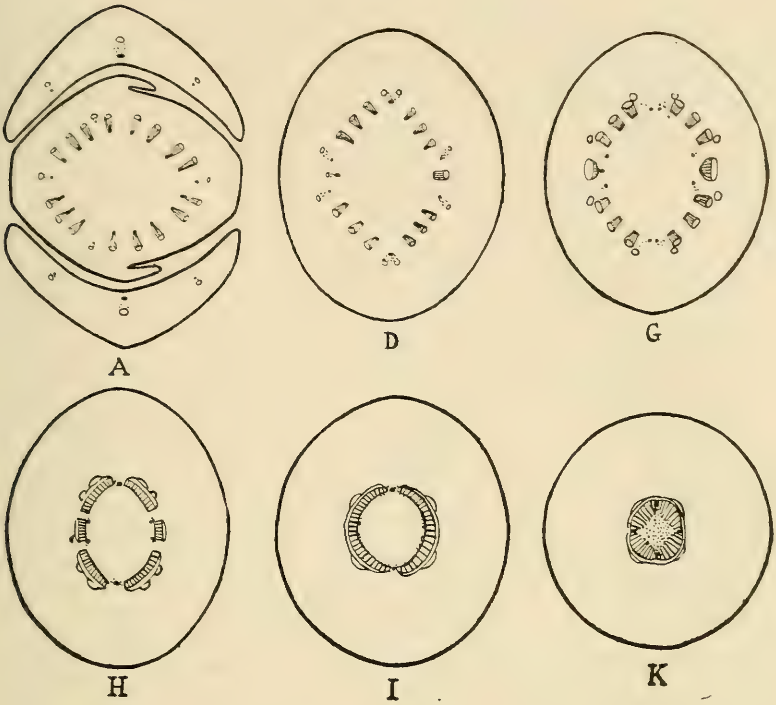
At the same time each pair of approximated phloem groups unite into a single group, then the lateral xylem groups twist into the usual root position, and considerably lower each pair of lateral xylem groups unite to complete the regular tetrarch stele of the root (j). It is to be noted that the vascular structures derived from the respective cotyledons remain distinct throughout the entire transition area of the hypocotyl, and unite only at the beginning of the root.

Throughout the hypocotyl the vascular tissue gradually approaches the center, and by the beginning of the root the pith is reduced to a small group of cells, which a little lower disappears entirely, and gives place to metaxylem (k).

As may be expected from the function and behavior of the cotyledons, their bundles, throughout, have a comparatively large amount of phloem, and correspondingly little xylem. The metaxylem, especially, consists even at a later stage of only a very few cells.



Text Figure 3. Diagrams illustrating the primary structure of the hypocotyl. × 25.



Text Figure 4. Diagrams illustrating the structure of the hypocotyl after growth of the epicotyl has taken place. × 15. The letters correspond with those in text fig. 3

By the time that the protoxylem is well developed in the cotyledonary bundles throughout the hypocotyl, differentiation of vascular tissue begins to occur in connection with the slowly developing epicotyl. A ring of small celled meristem surrounding a small pith develops in the epicotyl, and extends down into the upper part of the hypocotyl. A little lower, this ring becomes elliptical, and then separates into two parts with gaps opposite the median bundles of the cotyledons. Downward the half ellipses of plerome tissue pass out farther from the center, and break up into strands which stand just inside of the gaps in the ring of cotyledonary bundles. The end strands of each half ellipse may join the meristem tissue in the middle of the corresponding median cotyledonary bundle (d). All the other epicotylary strands, with a single exception, end blindly about the level where the cotyledonary bundles begin to

twist into the root position (e, f). The exception is the strand which corresponds to the middle of the first epicotylary leaf. This stands opposite to the sinus between the cotyledons on one side of the seedling. This bundle extends considerably farther down the hypocotyl than any of the other epicotylary strands (f, g.). It is also exceptional in the early differentiation of its primary tissues. Protoxylem develops early in the lower part of its course, and it forms for some distance a small but conspicuous bundle of the ordinary stem type standing between the two lateral xylem strands on one side of the hypocotyl. Like all the other epicotylary bundles it ends blindly at the bottom.

Secondary Thickening of the Hypocotyl.

There is no secondary thickening in the cotyledonary bundles down to the level of the insertion of the epicotylary structures (Text Fig. 4, a, d, g). In the epicotyl, on the other hand, the zone of meristem serves as a cambium which develops a ring of bundles, the elements of which are almost entirely secondary. These epicotylary bundles pass down between the cotyledonary bundles in such a way that one stands on each side of the hypocotyl between the two lateral xylem strands and two or three in each of the spaces between a lateral xylem strand and the adjacent median bundle (g).

Continuous with this epicotylary cambium, a cambium layer develops in the lower part of the hypocotyl between the separating groups of primary xylem and phloem (h, i), and thence downward into the root where it occupies the ordinary position. This cambium in the lower hypocotyl and root produces continuous secondary xylem so that the epicotylary bundles as they pass downward widen out, fuse with one another and with the primary xylem of the hypocotyl into a zone, at first interrupted over the primary xylem of the median bundles, a little lower closing over these regions, and finally as the root is reached, forming a solid central cylinder.

It will thus be seen that the connection between the vascular tissue of the epicotyl and that of the root is accomplished almost entirely by the secondary thickening of the hypocotyl, and that in this region a solid zone of secondary xylem is formed, points the more notable in view of the facts that secondary thickening is not strong-

ly developed in *Caulophyllum*, either in the stem or in the root, and that neither in the rhizome nor in the aerial stem of the plant do the bundles fuse into a zone as is usual in dicotyledons, but they remain permanently distinct, a condition which obtains not only in *Caulophyllum*, but generally throughout the *Berberidaceae* and also in many other families of the *Ranales*.

Summary.

The seed and seedling of *Caulophyllum thalictroides* show several marked peculiarities of form, structure, and behavior.

The ripe seed consists of a fleshy testa enclosing the very hard endosperm, of peculiar form, which in turn encloses the small embryo. The inner integument almost entirely disappears as the seed ripens.

The embryogeny differs from the ordinary dicotyledonous type rather in the earlier than in the later stages. The embryo develops at first, with very little differentiation of tissues, into a pear-shaped protocorm with a massive suspensor. The cotyledons appear late in the development of the embryo. They are independent in origin, and are symmetrically placed. They display no unusual features of structure or form in the ripe seed, and bear stomata despite their entirely hypogean life.

The germination of the seed is very slow, consisting at first of the gradual intraseminal growth of the embryo, then of a season's extraseminal growth, which is usually entirely hypogean, and is supported by the large store of nutriment in the endosperm. During this growth the blades of the cotyledons together form a peculiar haustorial organ which digests and absorbs the endosperm.

The first leaves of the epicotyl are usually scale like, and serve to enclose a winter bud.

The vascular system of the seedling is of a typical tetrarch type, each cotyledon furnishing three bundles to the hypocotyl, of which the middle one shows a double structure in the hypocotyl. The vascular tissues coming from the two cotyledons remain distinct almost throughout the hypocotyl.

The hypocotyl undergoes a very considerable secondary thickening which results in the formation of a continuous zone of xylem surrounding the pith,—a structure not found elsewhere in the plant. By means of this secondary thickening the vascular tissue of the epicotyl is brought into connection with that of the root.

Explanation of Plates.

Plate IV. Figure 1. Young ovule about three weeks before the flowering period. Megaspore mother-cell in synapsis. × 400.

2. Inner part of ovule a few days after flowering, showing one-celled embryo, developing endosperm, including the peculiar antipodal portion, *a*, the nucellar remains *n*, *n'*, the inner integument, *i*, and part of the outer integument, *o*. × 290.

3-9. Early stages in the development of the embryo. × 950.

10. Antipodal end of embryo-sac of a seed about three weeks after flowering, showing the relation of the structures of the embryo-sac to the chalazal vesicle. × 300.

Plate V. Photomicrographs of the embryo.

11. Micropylar end of the embryo-sac about one month after flowering, showing small embryo. × 200.

12. Embryo in seed about seven weeks after flowering showing the beginning of the cotyledonary mounds. × 100.

13. Slightly older embryo. × 100.

14. Embryo with well developed cotyledons, about two months after flowering, showing differentiation of plerome, periblem, root-cap, and epicotylary meristem. × 100.

15. Longitudinal section, perpendicular to the plane of the cotyledons, of an embryo from a nearly ripe seed, three months after flowering,—*r*, growing point of the root, *e*, epicotylary meristem. × 50.

16 and 17. Two longitudinal sections of an embryo from a ripe seed, taken parallel to the plane of the cotyledons, *s*, stomata, *e*, as in fig. 15. × 50.

18. Embryo from seed which had germinated for fourteen months. × 50.

Plate VI. Seedlings of the first year's extra-seminal growth.—Photographs, natural size.

19 and 20. The usual method of germination.

21. Same seedling as fig. 19 with part of the seed removed to show the haustorial part of the cotyledons.

22. Same seedling as fig. 20 removed from seed.

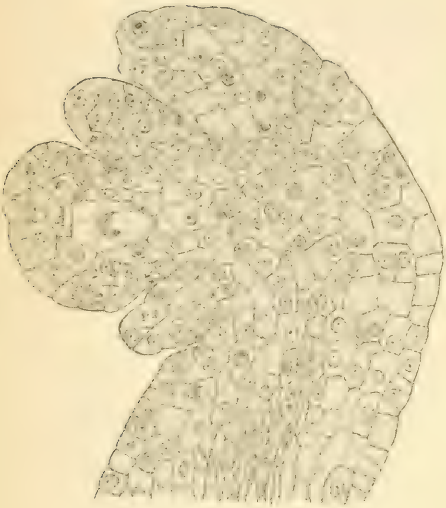
23. Unusual type of germination in which a foliage leaf is developed the first year.

Plate VII. Seedlings of the second year's extra-seminal growth.—Photographs, natural size.

Plate VIII. Seedlings of third and fourth year's growth. × 2/3.

Plate IX. Seedling about ten years old, showing the still functional primary root, the development of secondary roots from the rhizome, and the branching of the rhizome. × ½.

Plate X. Photograph of reconstructed models of embryos at about the age shown in figs. 12 and 13. Plate V. × 100.



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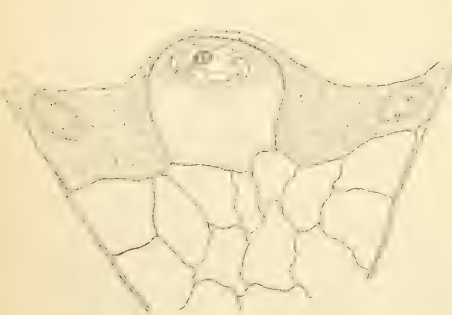

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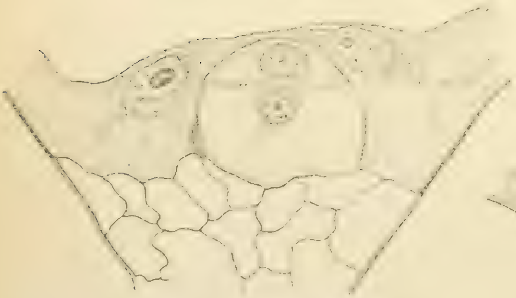

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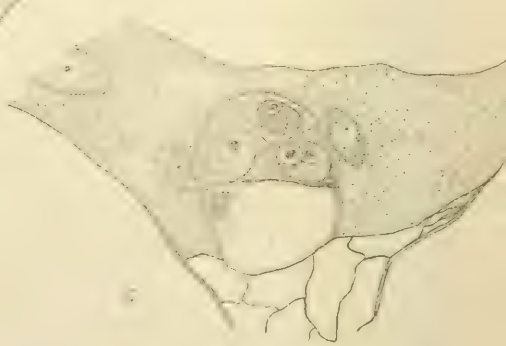

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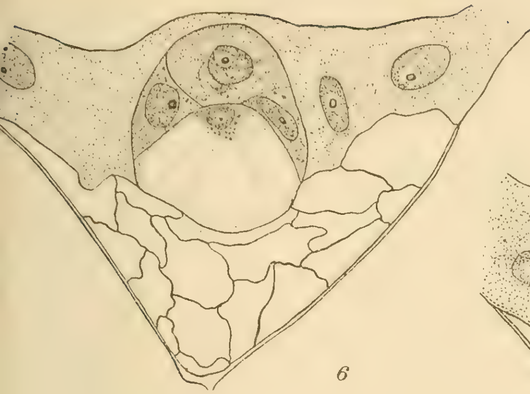

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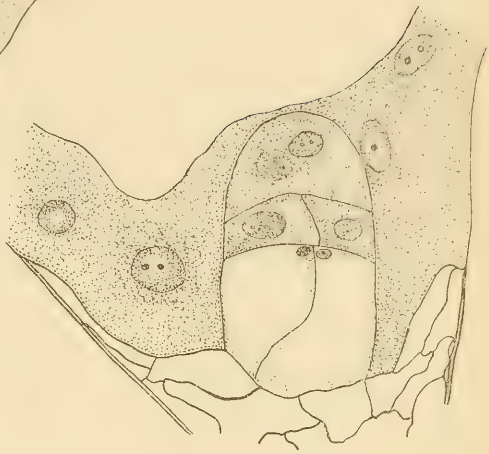

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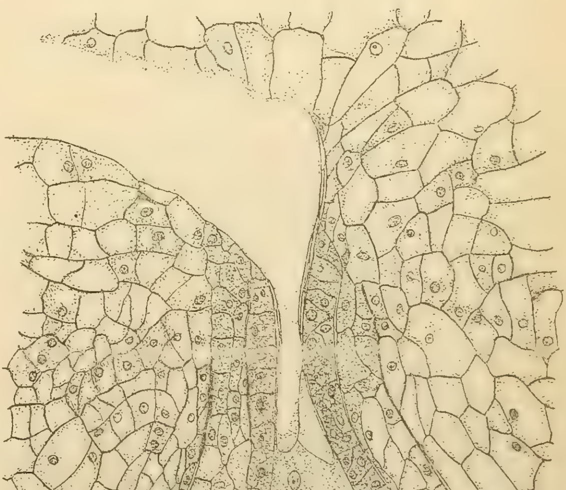

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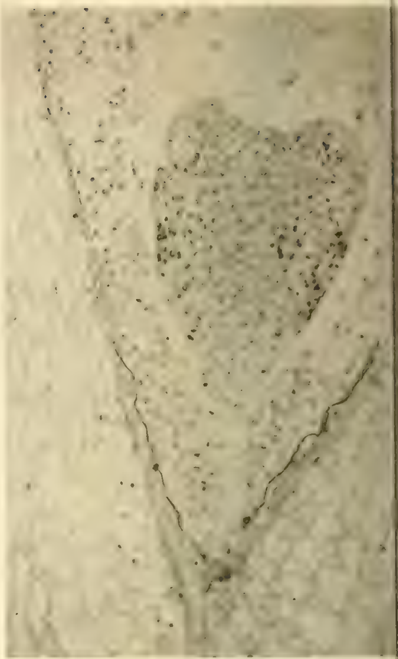

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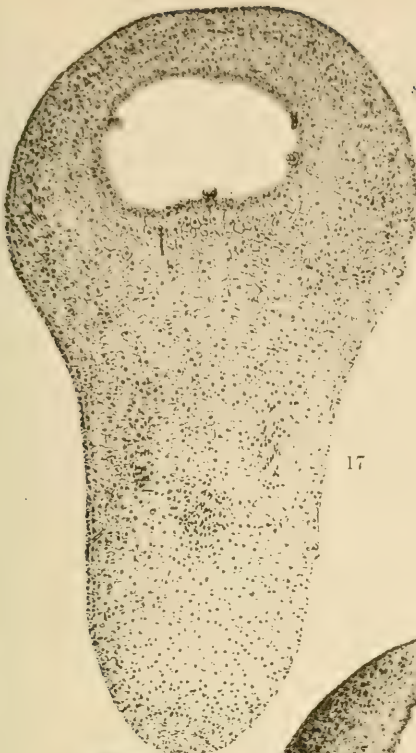

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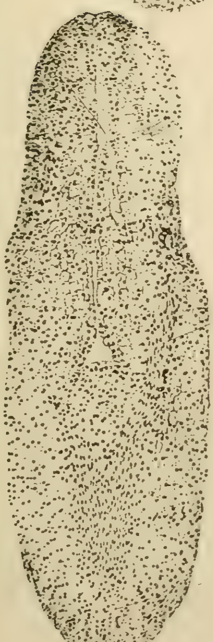

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E V.

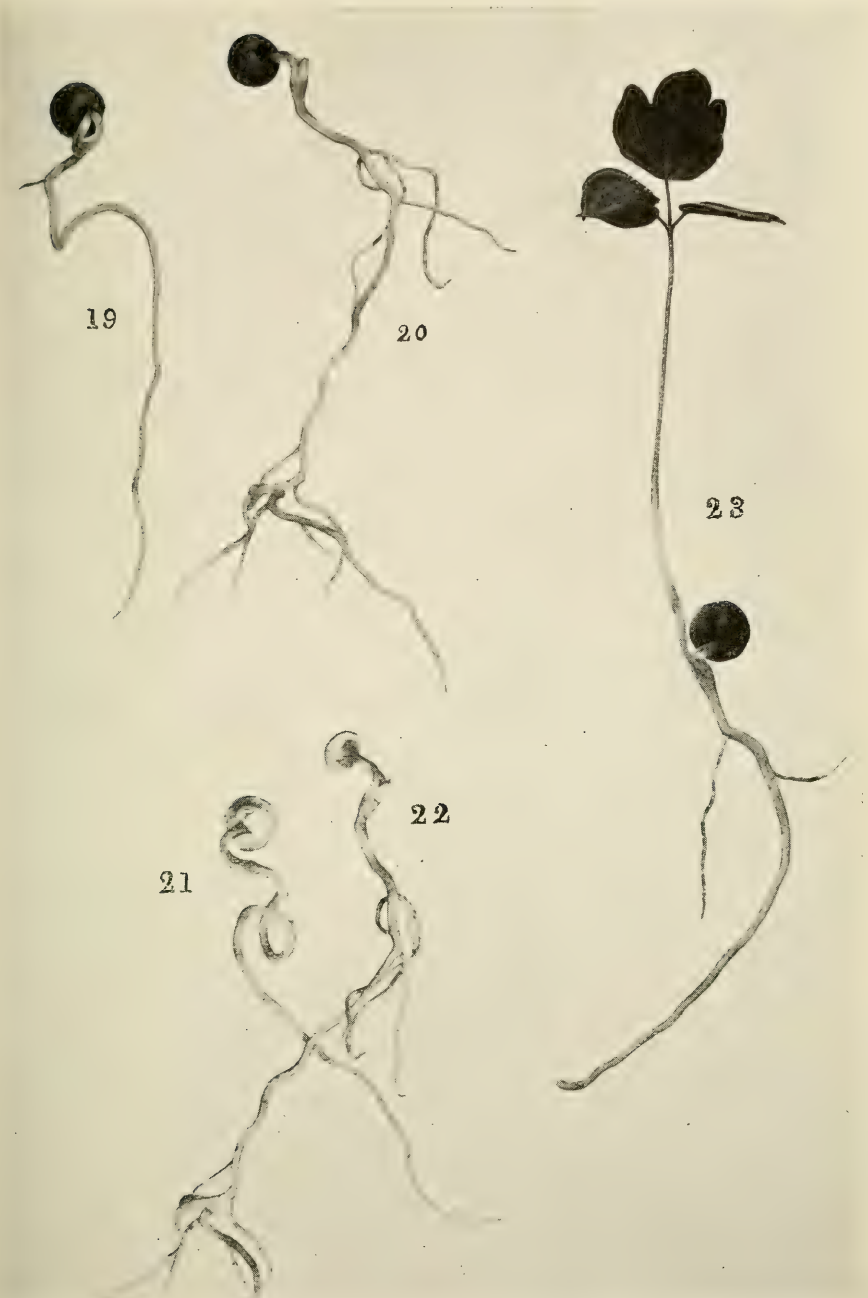

PLATE VI.

PLATE VII.

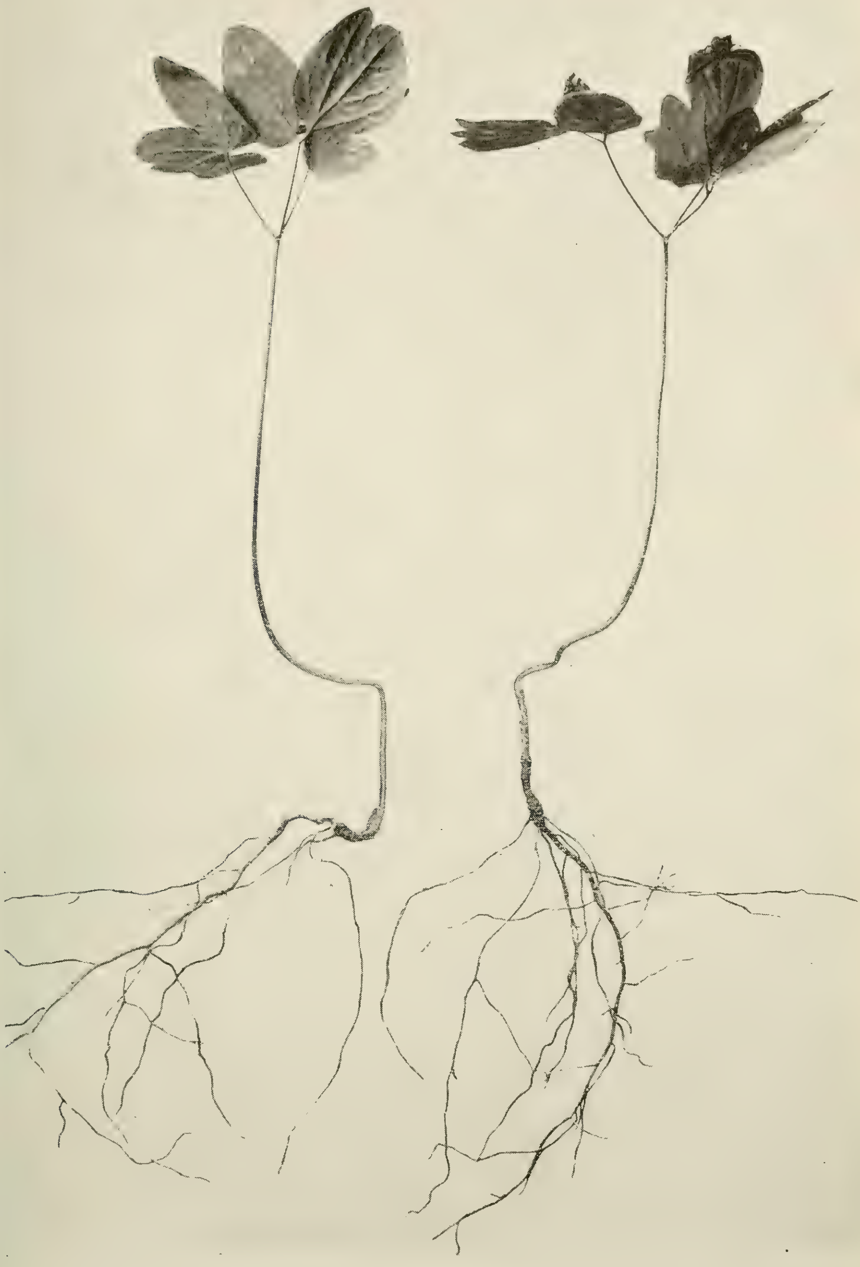

PLATE VIII.

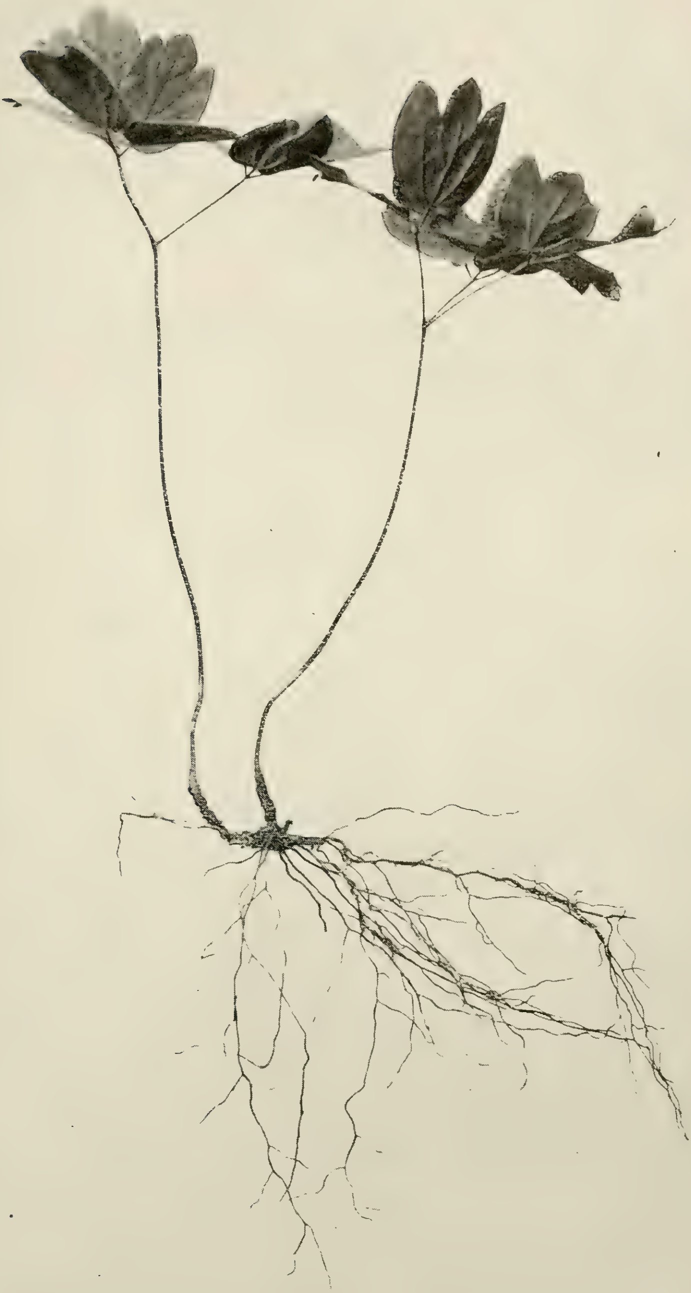

PLATE IX.

PLATE X.

3. INFLUENCE OF PHYSICAL FACTORS ON TRANSPIRATION.

ARTHUR WILLIAM SAMPSON
and
LOUISE MARIE ALLEN.

INTRODUCTION.

Transpiration, as a continuous and important physiological function of the plant, which is readily measurable, has long been an interesting and important subject for investigation. As a rule, however, investigators have confined themselves to the measurements of transpiration independent of its relations to physical factors. Where the latter have been considered at all it has been in a more or less general way. The aim of the present paper has been to measure transpiration along the following lines:

1. To determine the individual variation of the same species grown and tested under the same conditions.
   (a) In the plant house;
   (b) In their natural habitats.
2. To measure individuals of the same species, some of which had developed in the shade and some developed in the sun.
3. To determine the effect of altitude and pressure on this function.
4. To determine the relation between the internal structure and the transpiration of an amphibious plant, and to compare it with the internal structure and transpiration of land plants.
5. To test the effect of some of the common acids and alkalies on this function.
6. To study the effect of three common soil types and the influence of soil textures.

It would seem that transpiration determined along these lines should give results of value both from the theoretical and practical side. For a study of sun and shade forms of the same species, no plants could be more suitable than those developed in the vari-

ous habitats found in the vicinity of the Alpine Laboratory at Minnehaha, Colorado, where the light, temperature, humidity, and soil moisture content are extremely variable in the different habitats.

The major part of the investigation was carried on in the Department of Botany of the University of Nebraska, and at the Alpine Laboratory at Minnehaha, under Dr. F. E. Clements. The minor investigation of the effect of soils was done independently by Arthur W. Sampson, in the Department of Agronomy, Division of Soils, under Prof. Alvin Keyser. The physical factors cited in the various formations at the Alpine Laboratory are those determined by Dr. Edith Clements.[1] Grateful acknowledgment is made for their use. Helpful suggestions were made from time to time by Dr. C. E. Bessey and Dr. F. D. Heald, and appreciation is here tendered for the facilities offered by the Department of Botany at the University of Nebraska, and at the Alpine Laboratory, Minnehaha, Colorado.

Working Plan.

No mode of determining the loss by transpiration is free from error. The method of measurement resorted to with all alpine forms was by weighing leafy twigs with the cut ends immersed in water. Several vials were used with tightly fitting corks having a perforation in the centre through which the stem was inserted. The corks were tightly sunk below the mouth of the vial, and the depression filled with a mixture of vaseline and plaster paris, about the consistency of gum. Over the top of the vial and fitting closely around the stem was stretched a piece of rubber tissue.

Weighing the leafy stems with the cut ends immersed in water in this way, is not likely to afford the same absolute amounts of loss by transpiration as would be given by the same twigs supplied with water by the normal root pressure of the plant. But the leaves are in a normal atmosphere, and their relative losses (as compared with each other) may be very nearly the same as under absolutely natural conditions. Besides, the use of the potometer is indispensable where one wishes to determine the loss by transpiration of trees or shrubs where only a part of the plant can be used. In no case were weighings made after the leafy stems had been in potometers more than four days, or after the leaves showed the slightest signs of wilting or drying.

In the plant house the pot method was used entirely, the soil

[1] Relation of Leaf Structures to Physical Facts, 1905.

being so enclosed as to allow no loss of water except through transpiration. Seeds were sown in flats and the young seedlings transplanted into pots. For individual measurements only one plant was grown in a pot, but in working with soil types and textures where wheat alone was used, four plants were grown in the pot.

For the soil tests, earthern pots dipped in hot paraffin were used exclusively. The water content of the soil in the pots was kept as constant as possible. No additional water was added to the soil during the experiment. In the case of either wire or earthern pots, the tops were covered by parchment paper which had been dipped in hot paraffin. The paper was cut to fit the pot and tightly sealed by running paraffin around the edges.

Only the leaves were considered as transpiring surfaces, since it was found that the stems lost only two to three per cent of the total amount. Leaf areas were determined first by simply tracing the leaves on paper and cutting out the traced portion. Several units of paper were weighed, an average taken, and the area calculated. Later photographic prints were made of the leaves, using solio printing paper. The white portion representing the leaves was cut out and weighed. Knowing the weight of one square decimeter of solio paper, the area was readily calculated. The area thus obtained is, of course, that of one side of the leaf only, and must be doubled for the total area.

Several weighings were made to determine the uniformity in weight of the paper, and an average of the readings was used throughout. The readings and average thereof are shown in the following table:

Solio per sq. dec....................	No. I	1685 mg.
Solio per sq. dec....................	No. II	1692 mg.
Solio per sq. dec....................	No. III	1690 mg.
Solio per sq. dec....................	No. IV	1693 mg.
Solio per sq. dec....................	No. V	1694 mg.
Average		1690.8 mg.

From the above average, 16.9 mg. was taken as the weight of 1 sq. cm. of paper. The weight of the leaf prints divided by 16.9, *i. e.*, the weight of 1 sq. cm. multiplied by 2, gives the leaf area in square centimeters.

STOMATA. In all plants used, stomata counts were made[1] by peeling off a small part of the epidermis. An ocular micrometer marked off in quadrants was used, making it possible to get an accurate count. Three counts were made on each leaf, one reading

[1] Exception—*Holidiscus.*

being made at the tip, one at the midrib, and one near the base. An average of the readings was taken for the number of stomata found on the leaf in question. Measurements of the stomatal openings were also taken when possible.

The tables which follow have the measurements of the physical factors above, immediately under which will be shown the behavior of the plants with respect to their water loss.

Individual Variation.

The three following tables show the variation found in *Helianthus* plants grown and tested in the plant house under the same physical conditions. All weighings were made in each series twice daily, at six a. m. and at six p. m. The measurements were begun February 25 and closed February 28, 1907. The plants in Series I were eight weeks old, and had an average leaf area of 86.29 sq. cm. Series II were five weeks old with an average leaf area of 28.658 sq. cm. Series III were three weeks old with an average leaf area of 12.73 sq. cm. Only the cotyledons were developed in this series, the true foliage leaves having just started. The number of stomata in Series I and II were practically the same. On the upper side there were 270, on the lower side, 214. In Series III there were 196. stomata on the upper side and 280 on the lower. In all the tables that follow, water loss is given in grams, except where otherwise indicated.

The physical factors given are an average of several readings taken during the experiment, and are as follows:

Light	.59
Temperature	61°
Humidity	55%

TABLE I.

SERIES I			CHECK		
No.	*Day Loss*	*Night Loss*	*No.*	*Day Loss*	*Night Loss*
1	42.16	18.21	1	40.62	19.38
2	44.93	21.31	2	43.26	18.46
3	47.22	19.26	3	44.57	21.39

SERIES II			CHECK		
No.	*Day Loss*	*Night Loss*	*No.*	*Day Loss*	*Night Loss*
1	50.32	24.28	1	54.32	24.62
2	54.11	25.38	2	51.65	24.41
3	52.04	23.42	3	49.73	26.33

SERIES III			CHECK		
No.	*Day Loss*	*Night Loss*	*No.*	*Day Loss*	*Night Loss*
1	56.78	24.79	1	55.52	24.05
2	58.41	27.92	2	55.48	28.33
3	58.22	27.84	3	58.73	24.24

A comparison of the tables indicates that the young *Helianthus* with cotyledons lost more by transpiration than did the older leaves. On the contrary, the number of stomata on the upper side of the cotyledons are fewer per square millimeter than they are on the foliage leaves. The loose spongy tissue and poorly developed cuticular layer found on the cotyledons probably accounts for the greater loss of water.

Only slight variations occur in each series, the greatest being about 5 mm. The loss at night seems to be more uniform than in the daytime.

In selecting plants in the alpine formations to be used in potometers, great care was taken to get them as uniform in size as possible, and in a good healthy condition. Three plants of the same species were tested and two checks were made.

Potometers were set up August 17, and measurements closed August 20, 1906.

TABLE II.

Table of Physical Factors.

LIGHT	WATER CONTENT			HUMIDITY	TEMPERATURE		
	Saturation Point	Normal	Available		Air	Surface	Soil
1.-0.1	20%	6-9%	4.5-7.5%	30-65%	51-76°	80°	58°

PLANT	No.	Day Loss	Night Loss	STOMATA No. per sq. mm. Above	Below	Size Opening Above	Below
Wagnera leptosepala	1	16.6	9.2		62	....	16.8×2.8
"	2	19.0	8.0				
"	3	17.2	8.6				
Apocynum androsaemifolium	1	10.8	8.10		473		5.6×.8
"	2	12.2	7.2				
"	3	11.8	8.6				
Fragaria bracteata	1	18.2	11.0		187		5.1×.7
"	2	20.4	9.0				
"	3	19.6	12.6				
Populus tremuloides	1	18.8	8.8		71	....	......
"	2	14.8	11.8				
"	3	16.4	11.4				

PLANT	CHECK NO. I No.	Day Loss	Night Loss	CHECK NO. II No.		
Wagnera						
leptosepala	1	19.8	9.2	1	18.	10.1
"	2	19.0	8.8	2	21.4	9.1
"	3	18.8	8.2	3	19.3	8.8
Apocynum						
androsaemifolium	1	16.4	7.8	1	18.6	10.3
"	2	14.0	9.0	2	16.1	10.1
"	3	14.0	8.6	3	15.6	9.3
Fragaria						
bracteata	1	19.4	12.0	1	19.8	10.6
"	2	18.8	10.8	2	19.3	10.8
"	3	19.6	9.2	3	16.6	11.3
Populus						
tremuloides	1	14.4	9.4	1	15.8	10.
"	2	14.2	7.84	2	15.2	13.3
"	3	16.8	10.2	3	13.6	11.7

Both in the main table and in the checks only slight variations occur, not usually exceeding 3 mg. per square centimeter for a period of 12 hours. Therefore it may be concluded that plants of the same species grown in the same habitat when tested under the same physical conditions show but slight variation in transpiration per unit of surface exposed.

Periodicity in Transpiration.

For the purpose of determining the time of maximum and minimum transpiration during a day of twenty-four hours, three series of two plants in each were set up and tested. Series I were *Helianthus* plants four weeks old, Series II *Helianthus* eight weeks old, and Series III, barley plants three weeks old.

Weighings were begun at six p. m., February 16, and made hourly until six p. m., February 17. Physical factors, such as light, temperature, and humidity, were made between the hours. The day chosen for the experiment remained cloudy throughout, causing only slight variations in physical factors.

Curtis (Bull. Torrey Bot. Club, 1901, 28: 335) found that on cloudy days when the intensity of the light was quite uniform, or at least not in keeping with the time of day, the transpiration curve shows a pronounced maximum near midday. It was also characterized by minor fluctuations that occurred independently of climatic changes. An illumination of an electric light 900 candle power under uniform external conditions demonstrated a periodicity in the transpiration of several plants that correspond in the main with the curves determined on cloudy days.

The following table gives the loss for one square centimeter in milligrams for twenty-four consecutive hours.

TABLE III.

	Hour Day p. m. 6-7	8	9	10	11	Midnight 12	1	2	3	4	5	6
Light												
Temperature *in Centigrade*	24°	23.6	20	1.82	17	16.6	16.3	15	15	14.3	14	13.3
Humidity	56%	55	56	56	55	56	57	58	58	57	59	61
SERIES I												
Helianthus annuus Leaf area 15.38 sq. cm.	9.10	7.15	6.17	3.90	1.95	1.30	1.30	1.10	.91	1.23	1.56	4.55
Helianthus annuus Leaf area 13.11 sq. cm.	7.3	6.6	5.8	4.3	2.3	1.6	1.0	1.3	1.0	1.2	2.0	3.9
SERIES II												
Helianthus annuus Leaf area 152.29 sq. cm.	4.6	3.6	3.3	3.6	2.5	1.0	1.3	1.5	.8	.6	1.3	2.8
Helianthus annuus Leaf area 145.38 sq. cm.	5.36	3.85	3.98	3.23	2.26	1.65	1.37	1.10	.96	.96	1.85	2.75
SERIES III												
Barley Leaf area 6.44 sq. cm.	3.88	3.88	3.10	3.10	2.31	2.31	1.86	1.70	2.17	2.48	3.10	4.33
Barley Leaf area 4.49 sq. cm.	4.99	4.45	4.45	3.78	3.34	3.34	1.89	3.34	1.11	1.11	3.34	3.

TABLE III. (Continued.)

	7	8	9	10	11	Midday 12	1	2	3	4	5	6
Light	.003	.004	.005	.025	.036	.022	.022	.055	.016	.016	.008	.004
Temperature *in Centigrade*	14.3°	16.8	18.1	19	20	24	25.5	25.5	27	25	24	24
Humidity	62%	61	57	57	56	56	53	53	51	52	53	52
SERIES I												
Helianthus annuus Leaf area 15.38 sq. cm.	5.83	6.50	8.45	9.10	9.75	10.07	12.35	11.06	8.77	7.15	7.15	5.85
Helianthus annuus Leaf area 13.11 sq. cm.	6.1	7.0	8.3	10.	10.6	10.7	11.8	11.8	7.3	7.0	6.1	5.9
SERIES II												
Helianthus annuus Leaf area 152.29 sq. cm.	3	4.7	5.5	5.6	6	9.2	11.4	10.	7.1	3	3.2	2.5
Helianthus annuus Leaf area 145.38 sq. cm.	4.40	5.57	5.84	5.07	8.73	9.69	12.17	9.45	5.91	4.12	4.12	2.06
SERIES III												
Barley Leaf area 6.44 sq. cm.	5.43	6.21	9.0	9.03	20.65	27.48	14.44	11.80	11.49	9.31	6.21	6.21
Barley Leaf area 4.49 sq. cm.	5.56	8.90	11.13	12.61	22.23	31.18	16.70	14.03	13.14	11.13	7.79	7.79

From the above table it will be seen that loss by transpiration gradually decreases toward midnight. The maximum is reached from ten a. m. to two p. m. From that time on there is a decrease again.

Light reaches its maximum during the hour that the transpiration current is the strongest, while the percentage of humidity gradually decreases at that time. The temperature, however, does not reach its highest point until 3 p. m., after which it begins to decrease.

In order to correlate the criteria obtained with the hour of day and the physical factors, and to show more in detail the fluctuations in individual variation, curves have been plotted for the three series, using the figures given in the preceding table.

Effect of Light.

In order to determine the effect of light on transpiration, three shade tents were constructed in the plant house, using different weights of muslin. The plan was to have the darkest shade tent compare, with respect to light, to that of the most dense forest. The tables of physical factors, being an average of a great number of readings taken during the experiment, will give a good idea of the condition within the tents. Plants were measured in full light in the plant house and in the respective shade tents, weighings being made twice daily. The plants used were *Helianthus annuus* and *Cucumis sativus.*

From the table of physical factors it will be noticed that light is practically the only variable factor in the tents in question. The response of transpiration to this factor is found to be very pronounced.[1] A decrease in water loss of from six to eight milligrams is obtained by comparing Series I with Series II, their light intensities being .6 and .056 respectively. Series III with a light intensity of .0038 shows a decrease of about six milligrams as compared with Series II. Series IV with light .0012, a little less than half the intensity of Series III, has a decrease of from two to four milligrams per unit area.

[1] Schimper, A. F. W. *Plant Geography*. 1903, p. 4.

Fig. 2

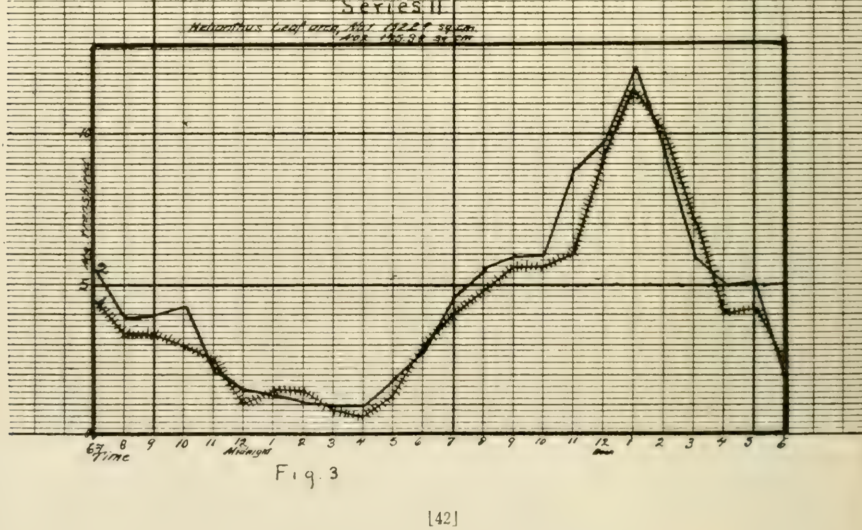

Fig. 3

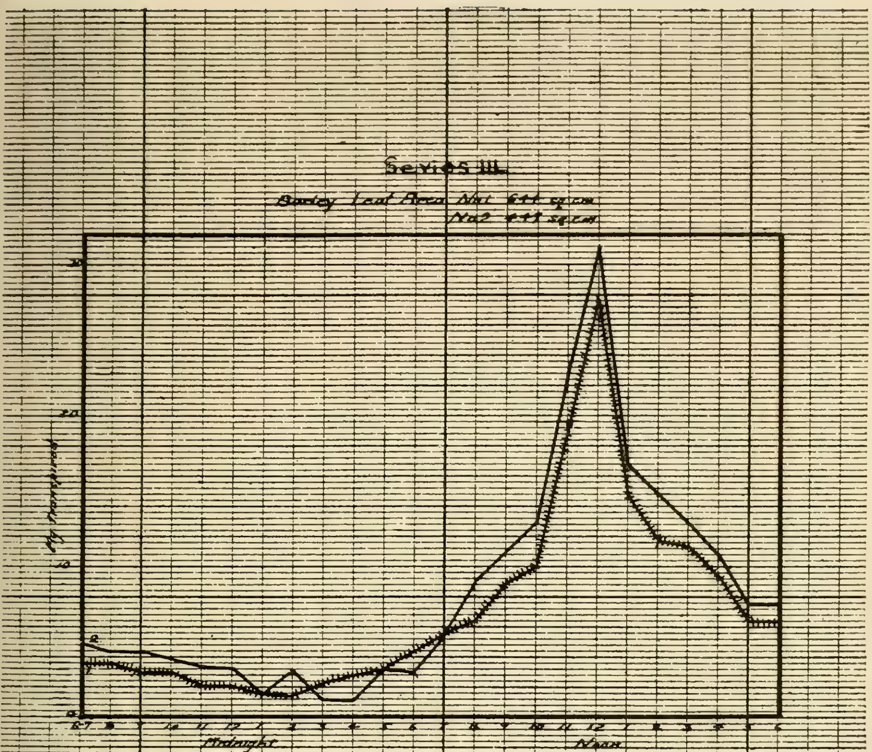
Series III.
Midnight
Noon

Fig 4

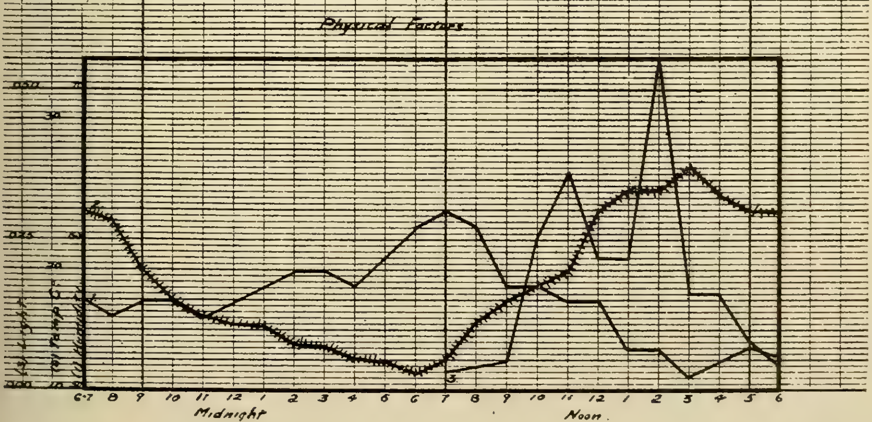
Physical Factors
6·7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6
Midnight
Noon.

TABLE IV.

TABLE OF PHYSICAL FACTORS.

	SERIES I Plant House	SERIES II Light Tent	SERIES III Medium Tent	SERIES IV Dark Tent
Light	.6	.056	.0038	.0012
Temperature	28.1	28.5	27.7	28.3
Humidity	55%	60%	60%	61%

Plant	No.	Day Loss	Night Loss	Day Loss	Night Loss
		SERIES I		CHECK	
Helianthus annuus ..	1	54.2	26.8	50.46	24.68
" ..	2	48.36	27.63	52.39	23.41
" ..	3	50.82	24.39	56.32	26.26
Average of all results obtained		51.93	27.	52.41	25.07
Cucumis sativus ...	1	43.51	18.52	40.49	17.6
" ..	2	40.4	17.68	43.86	18.
" ..	3	39.24	19.41	46.21	18.81
Average		41.26	18.5	43.4	18.48
		SERIES II		CHECK	
Helianthus annuus ..	1	46.38	19.61	44.22	20.
" ..	2	49.29	22.	47.29	22.31
" ..	3	45.2	19.11	48.1	20.8
Average		46.3	20.26	46.7	21.
Cucumis sativus	1	34.28	16.29	36.83	17.3
" ..	2	36.28	17.3		17.43
" ..	3	33.	17.72	33.68	18.
Average		34.5	17.1	35.2	17.6
		SERIES III		CHECK	
Helianthus annuus	1	39.8	18.22	38.20	19.5
" ..	2	36.23		36.	18.7
" ..	3	35.38	16.9	39.48	18.7
Average		37.1	17.5	37.9	18.6
Cucumis sativus ...	1	30.02	16.20	29.34	15.08
" ..	2	28.4	15.29	28.27	15.
" ..	3	29.	15.3	26.8	
Average		29.1	15.6	28.14	15.4
		SERIES IV		CHECK	
Helianthus annuus ..	1	30.2	15.	36.60	14.7
" ..	2	33.71	14.6	33.69	16.73
" ..	3	34.8	17.21	32.83	16.41
Average		32.9	15.93	34.4	15.8
Cucumis sativus ...	1	25.84	14.23	25.6	15.22
" ..	2	24.24	12.	26.2	14.17
" ..	3	27.7		24.81	13.18
Average		25.9	13.1	25.5	14.2

Comparative Transpiration of Polydemic Forms.

In order to correlate a relation between the behavior of polydemic forms, that is, plants growing in two or more habitats (see Fig. 5), as found near Minnehaha, Colorado, plants of both forms were set up in potometers and stationed in both sunny and shady habitats. As far as possible, sunny days were chosen for the observations, weighings being made twice daily as in previous experiments.

The results are as follows:

PHYSICAL FACTORS—

Light	.6
Temperature	63.5%
Humidity	52%

TABLE V.

SERIES I. Sunny Habitat.

Plant	No.	Day Loss per sq. cm. in mg.	Night Loss per sq. cm. in mg.	STOMATA No. per sq. cm. Above	Below	Size of opening in Above	Below
Holodiscus australis—							
Sun Form ..	1	26.0	13.0				
Shade Form	2	19.12	11.2				
Quercus novi-mexicana—							
Sun Form ..	3	25.6	8.8		541		10.64×1.4
Shade Form	4	11.1	5.18		338		11.2 ×1.4
Allium recurvatum—							
Sun Form ..	5	38.4	13.16	78	72	19.6×2.8	19.6 ×2.8
Shade Form	6	23.0	9.4	65	64	12.6×1.4	14.0 ×2.8
Fragaria bracteata—							
Sun Form ..	7	19.4	6.8		164		
Shade Form	8	13.0	4.12		150		
Wagnera stellata—							
Sun Form ..	9	19.3	7.7		95		22.4 × —
Wagnera leptosepala—							
Shade Form	10	9.2	4.9		62		16.8 ×2.8

TABLE V. (*a*)

SERIES II.		Shady Habitat		Sunny Habitat (CHECK)		Shady Habitat (CHECK)	
		Day Loss per sq. cm. in mg.	Night Loss per sq. cm. in mg.	Day Loss per sq. cm. in mg.	Night Loss per sq. cm. in mg.	Day Loss per sq. cm. in mg.	Night Loss per sq. cm. in mg.
Holodiscus australis—							
Sun Form ..	1	21.12	14.8	30.6	16.8	24.4	16.1
Shade Form	2	17.8	8.0	19.8	10.0	14.8	10.4
Quercus novi-mexicana—							
Sun Form ..	3	18.8	4.6	23.6	9.2	20.7	3.20
Shade Form	4	8.0	3.92	14.6	6.4	9.56	4.84
Allium recurvatum—							
Sun Form ..	5	18.2	4.2	34.6	12.6	16.10	5.2
Shade Form	6	14.2	3.4	18.02	10.6	11.6	4.71
Fragaria bracteata—							
Sun Form ..	7	13.2	7.2	23.4	7.2	15.6	6.8
Shade Form	8	5.6	4.29	19.0	4.4	7.2	4.7
Wagnera stellata—							
Sun Form ..	9	20.4	4.8	18.9	9.2	17.9	5.7
Wagnera leptosepala—							
Shade Form	10	9.2	4.9	9.4	5.4	9.3	2.4

The ratio of transpiration of polydemic forms measured in both sun and shade is shown by the following table:

TABLE VI.

Formula: Loss of Sun Form / Loss of Shade Form.

I. Plants in their natural habitats	*Wagnera* Day	*Wagnera* Night	*Quercus* Day	*Quercus* Night	*Allium* Day	*Allium* Night	*Populus* Day	*Populus* Night	*Fragaria* Day	*Fragaria* Night	*Holodiscus* Day	*Holodiscus* Night
Maximum ..	2.7	4.5	3.2	2.7	2.7	4.3	3.81	3.62	3.3	1.7	2.0	1.7
Minimum ..	2.0	3.5	2.5	1.8	2.9	2.6	2.84	3.33	3.1	1.4	1.5	1.6
Av. of all values obtained	2.4	4.0	3.1	2.4	2.6	4.0	3.6	3.5	3.3	1.6	1.7	1.7
II. Both forms in sun—												
Maximum ..	2.4	1.8	2.3	1.8	2.0	1.5	2.2	4.4	1.4	1.7	1.5	1.6
Minimum ..	2.02	1.6	1.7	1.5	1.6	1.2	2.0	2.2	1.2	1.7	1.6	1.2
Av. of all values obtained	2.3	1.8	2.2	1.5	2.0	1.4	2.1	3.2	1.4	1.5	1.5	1.4
III. Both forms in shade—												
Maximum ..	2.8	3.0	2.3	1.4	1.5	1.3	3.1	2.83	3.7	1.7	1.6	1.8
Minimum ..	2.0	2.5	.6	1.1	1.3	1.0	2.0	1.0	2.2	1.4	1.1	1.4
Av. of all values obtained	2.5	3.0	1.6	1.3	1.3	1.3	2.6	2.5	3.2	1.5	1.4	1.5

From the foregoing tables it is evident that sun forms transpire more than shade forms. This not only holds when the plants are measured in their natural habitats, but also when both forms are subjected to either sun or shade. With both forms in their natural habitats, the sun form loses from one and one-half to four times as much as the shade form. With both forms in the sun, the sun form loses from one and one-half to three times as much as the shade form. When both forms are subjected to shade, the transpiration in the sun form is from one and three-tenths to three times that of the shade form.

These results are quite at variance with what would be the *a priori* opinion of botanists in general.[1] However, the greater transpiration of the sun form is accounted for, in part at least, by the greater number of stomata per unit of leaf surface as compared with the shade form. Further, the greater amount of chlorophyll in the tissues and the consequent greater activity partially explains the greater transpiration of the sun form.

A still further investigation on the effect of transpiration in various habitats was conducted at the Alpine Laboratory. Four stations were selected on the merits of their contrast in physical factors. Four different species with five plants of each were measured in potometers in these habitats and two checks made in each case. The following tables show the measurements of the physical factors in the respective habitats and an average of all transpiration results obtained.

TABLE VII.

PHYSICAL FACTORS.

Formation of habitat	Light	Water-Content			Humidity	Temperature		
		Saturation point	Normal	Available		Air	Surface	Soil
Station I— Brook Bank	.02%	.51%	35-40%	25-30%	72%	58°	55°	50°
Station II— Gravel Slide	.6	15	5-6	2.5-5.5	48	62	100	68
Station III— Spruce Forest	.03	45	18-22	12-16	55	60	62	51
Station IV— Half Gravel	.6	20	6-9	4.5-7.5	43	63.5	63	58

[1] Weisner, *Biologie der Pflanzen*, 1902, p. 11.

TABLE VII. (Continued.)

Plants	Station I Day loss	Station I Night loss	Station II Day loss	Station II Night loss	Station III Day loss	Station III Night loss	Station IV Day loss	Station IV Night loss
Apocynum androsaemifolium	9.2	7.6	16.2	12.2	19.9	8.5	19.9	14.8
Wagnera leptosepala	12.3	8.2	18.3	9.5	17.5	10.9	16.7	9.6
Wagnera stellata	14.2	7.7	16.2	9.6	16.4	11.3	17.9	10.6
Arctostaphylus uva-ursi	13.6	8.8	18.6	12.5	14.7	9.1	23.0	12.5

From this experiment it is shown still more conclusively that water loss by transpiration increases with the intensity of light.

It will be observed that Stations II and IV have the greatest light intensity, the highest temperature, and the lowest humidity. The plants in these stations transpired the most, showing conclusively that this function varies with the physical factors.

Effect of Altitude on Transpiration.

The dwarfing of vegetation found in high alpine regions led to an investigation of the effect of altitude on transpiration. Three attempts were made to determine this by means of plants placed in potometers, two of which were not satisfactory, owing to adverse weather conditions. Simultaneous readings of physical factors were taken at three different altitudes, 1,900 m., 2,600 m., and 3,800 m. At the two latter, simultaneous measurements of transpiration of *Edwinia americana* and *Wagnera stellata* were taken, three plants of each species being used in each case. From an average of a number of readings it was found that the light intensity was practically constant, that the relative humidity increased with the altitude, and that the atmospheric pressure was decreased. The above results are corroborated by Clements after investigations carried on for several successive seasons. (Sci. 25:287, 1907). At 2,600 m. *Edwinia* lost 4.4 mg. while at 3,800 m. it lost 5.6 mg. In the former, *Wagnera* lost 3.9 mg. and in the latter, 4.3 mg.

That reduced pressure leads to increased transpiration is demonstrated in part by these data. In order to substantiate this conclusion the following experiment was carried on:

Six plants of *Helianthus annuus* were used, two under normal pressure, 28.9 inches, two under a pressure of 20 inches, and two, 15

inches. All were placed under bell jars. An aspirator was used to reduce the pressure, which was measured by an accurately adjusted aneroid barometer. All other factors were uniform and constant, so that variations in transpiration were caused only by the difference in pressure.

TABLE VIII.

	PRESSURE	LOSS	CHECK
	Normal		
1............	28.9 in.	2.57	2.64
2............	28.9 in.	2.61	2.59
3............	20. in.	3.43	3.41
4............	20. in.	3.50	3.48
5............	15. in.	3.61	3.60
6............	15. in.	3.56	3.53

These experiments, showing transpiration to be increased by a decrease in atmospheric pressure, contradict the theory of Bonnier, *i. e.*, that the increased transpiration in high altitudes is due to increased light intensity. (Compt. rend. de l'acad. des sc. Paris tom. CXI, 1890, II, p. 377.)

Transpiration of Scirpus lacustris.

A number of bog plants, because of their great reduction of leaf area and general external appearance, have been called bog xerophytes (Schimper, p. 17), in spite of the fact that a xerophyte is a dry soil plant and that these plants grow in a super-saturated soil. Such a plant is *Scirpus lacustris,* and it has afforded most interesting results.

These plants were taken from the edge of a pond during the winter and placed in earthern pots in the plant house. In order to provide conditions as nearly like those of the natural habitat as possible, the pots were submerged in an aquarium. When they had attained a growth of about one meter in length they were removed from the aquarium, their transpiration measured, and the following results obtained:

TABLE IX.

			CHECK	
No.	Day Loss	Night Loss	Day Loss	Night Loss
1	79.2	44.6	67.5	42.8
2	70.69	51.8	82.3	50.7
3	82.5	42.3	86.5	51.2
4	65.4	40.4	78.4	43.6

In order to get a more definite idea of the meaning of this table, consider the average loss of a mature *Helianthus annuus* under similar conditions. *Scirpus*, with 135 stomata per sq. mm., during the day lost on an average 74 mg. per sq. cm., while *Helianthus*, having from 270 to 284 stomata on each side, showed an average loss of 46 mg.

From a study of the structure of *Scirpus* it will be seen that it possesses typical hydrophytic characteristics, (Clements, Research Methods in Ecology, p. 126.). These characteristics are large intercellular spaces, diaphragms, reduction in the number of stomata, and lack of protection against excessive transpiration. A longitudinal section of one of these stems shows the division into many small chambers, with numerous cross partitions or diaphragms. An attempt was made to estimate the total area of this interior tissue, the total volume of the air-containing spaces, and to compare them with the exterior transpiring area and the volume of the entire conical stalk.

Counts were obtained from the longitudinal section, and the average number of the cylindrical chambers was found to be 126. It was calculated from cross sections, taken two inches apart from tip to base of the entire stem, that the average number of chambers was 26, giving the total number of 3,276.

At the same time the above counts were made, the average length and diameter of each cylinder was determined to be 4.4 mm. and .8 mm. respectively, thus making the total area of these chambers 45,864 sq. mm.

In addition to this inner transpiring area, the area of the diaphragm within each cylinder must be considered. These are composed of thin layers of irregularly drawn out cells with large spaces between them. In order to compute the amount of tissue in these diaphragms, counts were made of the number in each chamber and measurements of the area were made. The entire surface thus obtained was 65,520 sq. mm., giving 111,384 sq. mm. total inner transpiring surface. Comparison of this with 7,479 sq. mm., convex surface of the conical stalk, shows it to be fifteen times as great as the exterior transpiring surface.

Considering the volume of the entire *Scirpus* stalk and the volume of the intercellular air chambers, we find that .8 of the entire volume is composed of air spaces. This extreme hydrophytic structure should be satisfactory explanation for the great amount of water lost by this plant.

Effect of Some Common Acids and Alkalies on Transpiration

The response of transpiration to acids and alkalies has been studied by a number of investigators, whose results are contradictory. Burgerstein ("Die Transpiration der Pflanzen," 1904) has carried on the most extensive experiments along this line. In general, he found that weak acid solutions accelerated transpiration, and alkaline solutions when used extremely dilute also accelerated it, but when stronger solutions were added transpiration was retarded.

In the experiment here conducted only four acids and three alkalies were used, these being tested on two species of plants, *Helianthus annuus* and *Zea mais.* Half normal stock solutions were accurately titrated in the Chemical Laboratory.

Plants were tested both in potometers and in pots. In the latter case they were grown in a loam soil. Weighings were taken every twenty-four hours. The transpiration of plants in distilled water, in potometers and soil was taken as a basis of comparison. The table following gives summarized results of all readings made in these tests.

TABLE X.

	ZEA MAIS				HELIANTHUS ANNUUS			
Distilled Water	In Potometers 29.7 Per cent solution		In Soils 43.1 Per cent solution		In Potometers 42.6 Per cent solution		In Soils 62.3 Per cent solution	
	.065	.130	1.0	1.5	.065	.130	1.0	1.5
Acids—								
HCL.	31.2	32.3	44.7	44.9	43.5	43.2	63.3	64.6
HNO_3	30.8	30.9	43.8	46.2	45.1	44.8	64.8	65.2
$C_2H_4O_2 \cdot 2H_2O$	29.9	30.4	43.5	44.4	42.8	43.2	63.1	64.1
$C_2H_4O_2$	30.3	32.0	43.8	43.6	43.1	43.4	64.2	65.2
Alkalies—								
KOH	26.2	25.3	40.8	43.7	41.0	40.3	62.6	58.5
Na_2Co_3	28.3	28.1	43.0	42.5	42.8	41.9	61.2	60.
NH_4OH	24.4	26.3	42.2	41.8	40.1	41.7	59.3	60.3

That the acids and alkalies used in these experiments act as stimuli with respect to their influences on transpiration will be observed in the above data.

In every case in the summarized table the acids accelerated this function, while in the majority of cases the alkalies retarded it. In a *very* few cases weak alkaline solutions increased transpiration as compared with that of distilled water. This differs somewhat from that found by Burgerstein ("Die Transpiration der Pflanzen,"

p. 142), but usually there was no response unless the solution was made stronger, in which case the stimulus was a negative one. The criteria for comparing weak and strong acid solutions shows that the latter did not always accelerate transpiration more forcibly than the weaker solutions, contrary to the belief of most investigators. Fluctuating variations in transpiration were observed from time to time, some individuals being absolutely out of proportion to the behavior of a large number of similar plants which were tested in the same way and under the same conditions. Where extreme discrepancies of this sort occurred, the plants were discarded.

It must be borne in mind that in most experimentation of this kind, there will occur unexplainable variations, and the true results must be attained from the summation of a great number of experiments. The above discrepancies might not have occurred had the number of plants used been larger.

Relation of Soil Textures and Some Soil Types to Transpiration.

It was deemed of sufficient importance, in connection with the other lines of investigation, to grow plants in various soil textures and in some of the common soil types and test the response of transpiration to them.

Wheat plants were used throughout, four being grown in each pot. A Minnesota variety was selected, known as "Minnesota No. 66." Pure quartz sand was used for the work on textures. The soil particles were sifted through a series of screens, the size of the meshes being as follows:

Series I, 10 per square inch; Series II, 15; Series III, 20; Series IV, 40; Series V, 60, and Series VI, 80 per square inch.

Three pots in each series[1] were run both in the original and in the check. For all series the initial moisture content of the soils was about twelve per cent. For both this experiment and that of "Soil Types" the transpiration was determined daily for a period of nine days. The pots of all series stood side by side in the plant house, where they were subjected to exactly the same changes in temperature, light, humidity, and air currents. Only two plants were run in each type because of the great amount of labor required in separating them.

At the end of the experiment both series were photographed. The

[1] Exception: Series V and VI.

tops were removed by cutting just above the surface, the green weight taken, and leaf areas obtained in the usual way.

In the "Soil Type" series, dry weight and ash determinations were made of the leaves. In the duplicates, however, measurements were carried on as far as transpiration was concerned, but owing to the great amount of work involved, the other measurements were made for one series only and not for the duplicates. The results on the experiment with soil textures are shown in the table which follows:

TABLE XI.

	Day loss	Night loss	Green weight in mg.	Soil moisture	CHECK Day loss	CHECK Night loss	CHECK Green weight in mg.	CHECK Soil moist're
Series I.								
1	64.20	28.21	563.7	7.6%	65.32	26.13	468.2	7.2
2	60.32	26.96	556.	8.1	62.11	25.81	520.	7.9
3	61.11	26.38	458.8	8.	62.55	25.	488.	7.6
Series II.								
1	60.41	22.64	565.3	8.4	61.62	24.29	520.6	8.2
2	59.25	23.26	564.6	8.8	60.	23.46	498.3	8.6
3	59.92	25.84	564.1	10.1	59.73	22.18	561.	8.9
Series III.								
1	57.22	18.6	565.	8.9	58.2	20.	562.8	9.2
2	58.13	17.92	564.8	9.	56.	18.34	529.	8.6
3	55.19	19.0	561.3	9.2	56.21	18.96	539.9	9.4
Series IV.								
1	52.0	16.29	492.1	9.8	49.61	17.26	461.3	9.6
2	50.33	16.38	541.6	9.6	.....	.....	.....	...
3	48.93	15.92	561.2	10.2	47.38	16.31	499.6	9.8
Series V.								
1	46.37	15.41	620.1	9.6	44.22	.....	628.1	9.6
2	43.0	14.1	576.2	9.1	45.38	14.2	429.0	10.4
Series VI.								
1	43.67	12.66	499.1	10.7	40.4	12.2	542.0	10.8
2	42.1	13.47	538.7	10.2	41.3	12.94	598.7	10.3

THERE IS NO APPRECIABLE DIFFERENCE IN THE SIZE OR VIGOR OF THE plants grown in the various textures, as is indicated by Fig. 8 and by the green weight shown in the table. The amount of transpiration is greatest per unit area in the largest particles of soil, there being a difference of about eighteen milligrams per square centimeter in the two extreme types during the day, and about twelve milligrams at night.

The explanation for this phenomenon is that the physiological water content of the soil with larger particles is greater than that

of the finer soil[1] and the water is more easily available to the plant. Clements, in "Research Methods in Ecology," (p. 78) says that there is a pull exerted upon each water film by the soil particle itself. This pull apparently increases in strength as the film grows thinner, and explains why it finally becomes impossible for the root-hairs to draw moisture from the soil.

This property, like capillarity, is most pronounced in fine-grained soils, such as clays, and is least evident in the coarser sands and gravels. It seems to furnish the direct explanation of non-available water, and in consequence, to indicate that the physiological water of the soil is an immediate result of soil texture.

Soil Types.

Three soil types and their combinations, together with the pure types modified with compost, were used in this experiment. Series I consisted of (a) loam soil, (b) loam with one-fourth compost (bulk), (c) loam and one-fourth sand. Series II consisted of (a) clay soil, (b) clay with one-fourth compost, and (c) clay with one-fourth sand and Series III of a similar group of sand soils. Fig. 9 shows the typical growth of the plants in each series.

The following table represents an average of all values obtained:

TABLE XII.

Series		Green weight	Dry weight	Ash	Day loss	Night loss	Check: Green weight	Check: Day loss	Check: Night loss
I	*a*	950	115.4	13.3	62.7	24.4	910	63.2	23.6
	b	1740	173.3	20.2	58.2	20.1	1230	59.3	20.3
	c	860	86.4	10.1	61.5	26.3	834	62.8	25.7
II	*a*	620	70.6	8.9	61.5	23.2	649	59.6	24.6
	b	1386	156.2	18.6	56.7	17.9	1046	56.2	17.6
	c	665	74.5	9.6	61.2	26.2	640	60.0	23.1
III	*a*	505	63.4	7.6	66.4	32.4	543	65.1	29.2
	b	1028	126.2	17.2	64.3	28.8	766	64.5	27.5
	c	560	75.1	9.4	64.8	29.5	507	65.4	29.5

There appears to be a slight tendency for the transpiration per square centimeter to be depressed in the better soils. Series I (b), II (b) and III (b) are pure types with one-fourth compost added. Judging from the amount of green weight produced by them, they may be considered best media for the growth of wheat plants. The amount of transpiration per unit area is comparatively

[1] Hedgcock, G. C. The Relation of the Water Content of the Soil to Certain Plants, Principally Mesophytes. Rep. Bot. Survey Neb., 6: 48. 1902.

less in these cultures than any in the series. Another fact that is made clear is that for the types of soil investigated at least, the amount of transpiration is correlated with the green weight of the tops.

Summary.

A concise statement of all results obtained in this paper is given as follows:

1. Variation in transpiration per unit area for a given time is found to be but slight, for plants of the same species, when about the same age, grown and tested under similar conditions, whether in their natural habitats or in the plant house.

2. Of polydemic forms, when measured in their natural habitats, those developed in the sun lose from two to four times as much water as those developed in the shade. When the two forms are placed in a sunny or shady habitat, the inequality of their transpiration is about as manifest in the sun as in the shade. This inequality is largely explained from the fact that the sun form has usually from twenty to sixty per cent more stomata per unit leaf surface than the shade form. The greater activity which takes place in the sun form also accelerates this function.

3. Other things being equal, an increase in altitude stimulates an increased transpiration. This acceleration is not due to an increased light intensity and a lower air humidity as is generally conceded, but is due to decreased pressure. This conclusion is further substantiated by the fact that when plants were subjected to various pressures under controlled conditions, the greatest transpiration took place where there was least pressure.

4. The transpiration of *Scirpus lacustris*, a "bog xerophyte," is almost twice as great as that of *Helianthus annuus*, a typical mesophyte with characteristic palisade and sponge tissue. This is readily explained by the great amount of transpiring tissue to be found in *Scirpus*. The external surface protected by an epidermis is fifteen times less than the inner transpiring tissue. Of the total volume of the stem, four-fifths is composed of air chambers. The number of stomata is reduced, and the only xerophytic characteristic is its leafless stem.

5. Generally speaking, acid solutions accelerate transpiration and alkaline solutions retard it, as compared with plants in distilled water. In a very few cases extremely weak alkaline solutions were found to increase transpiration. Transpiration often shows as

marked response to weak solutions of acids and alkalies as to stronger ones.

6. Plants lose more water by transpiration for unit area when grown in soils of coarse texture than when grown in soils of fine texture. It is probably due to the fact that the physiological water of the coarse soils is greater than that of the finer soils. Soil texture seems to have nothing to do with the amount of green weight produced.

There appears to be a slight tendency for transpiration to be depressed in the better soils. Also a correlation can be seen between transpiration and the green weight of the tops.

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4. TWO BASIDIOMYCETES NEW TO MINNESOTA: EXOBASIDIUM MYCETOPHILUM AND CANTHARELLUS RETIRUGUS.

Daisy S. Hone.

The above species appear rarely, not only in Minnesota but in the other parts of the United States. They both exhibit interesting and somewhat uncommon features in their habits. *Exobasidium mycetophilum* (Peck) Burt has been collected in several localities in the United States but this is the first collection from Minnesota. As far as the writer has been able to determine, this is the first collection of *Cantharellus retirugus* (Bull.) Fries in the United States.

Specimens of both species are in the collections of the Museum of the University of Minnesota. The drawings were made with the aid of an Abbe camera lucida from material preserved in formalin. Photographs of Plate XI. and XII. Fig. 1, were taken by Mr. C. J. Hibbard, formerly on the staff of the Minnesota Geological and Natural History Survey. Photographs of Plate XII. Fig. 2, 3, were taken by Mr. J. A. Gleen of Albany, New York.

I wish to thank Dr. E. M. Freeman for his suggestions and advice in preparing this paper.

Exobasidium mycetophilum (Peck) Burt.

While collecting in Crow Wing County, Minnesota, during July 1904, the writer discovered a large patch of *Exobasidium mycetophilum* (Peck) Burt. The collection was made on an island in "White Fish Lake" in Crow Wing County in the central, northern part of Minnesota. The island was covered with a heavy hardwood forest.

The large masses, consisting of convoluted, gelatinous to fleshy substance, white to yellowish in color, covered with a fine white powder, were found growing upon the cap and stipe of *Collybia dryophila* Bull. The fungus masses have very much the appearance

of a *Tremella* and were so large that they extended in folds over the surrounding chips and earth in which the *Collybia* was growing. One mass was four inches in diameter. The *Collybia* was growing abundantly among the decaying debris of a large water soaked log and was covered over with the white convoluted mass of *Exobasidium*.

Peck and Atkinson have both described this fungus from New York collections under the genus *Tremella*. Peck's [1] picture agrees perfectly with some of the very young masses of the Minnesota material, while Atkinson's [2] picture agrees with some of the slightly older stages. Burt [3] has published a more complete description from material collected in Vermont under the title, "Structure and Nature of *Tremella mycetophilum* Peck." He has clearly pointed out the structural characters of the basidia which separate this from the *Tremella* type and has placed it in the genus *Exobasidium*. The Minnesota specimens distinctly confirm this classification but the basidiospores are very much smaller and more nearly spherical in shape than those described by Burt. In the mature Minnesota material the spores are not more than 2-3 mic. in diameter and nearly spherical (Pl. XIII. Fig. 4, 6). In fact they agree more nearly with Burt's conidia than with the basidiospores. As they are repeatedly found attached to the basidia, there can be no doubt as to their origin.

The fungus does not appear to form a true gall, although it appears to be a true parasite. There seems to be no hypertrophy of the host although it is sometimes difficult to distinguish the hyphae of the host from those of the parasite. The attachment to the host is very slight, especially on the stipe (Pl. XIII. Fig. 5) where it grows just as abundantly as on the cap. On the stipe the fruiting body seems to be merely pushed out between the hyphae of the host, thence swelling out into a hollow convoluted mass. The hyphae are smaller and more finely granulated generally, than those of the host plant and are from one-half to one-quarter as wide. Clamp connections are found only among the coarser sterile hyphae below the hymenial layer.

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[1] Peck, ... N. Y. Mus. Report 28 : 53, pl. 1. f. 4. 1879.

[2] Atkinson, .. "Mushrooms Edible, Poisonous & etc." p. 205. 1900.

[3] Burt, E. A. Bull. Torr. Bot. Cl. 28 : 285-287. pl. 23. 1901.

The Minnesota specimens differ from those described by Burt: (1.) in the much larger convoluted masses, some being four inches in diameter, (2.) in the nearly spherical and much smaller basidiospores, 2-3 mic. in diameter.

Cantharellus retirugus (Bull.) Fries.

This fungus was first classified by Gmelin in Linnaeus' "Systema Naturale" 2: 1401 (1735), as *Merulius reticulatus*. Since then it has been described by Bulliard in his "Champignons" p. 289 (1791), as *Helvella retiruga* and by Persoon in his "Synopsis" p. 494 (1801) as *Merulius retirugus*. Fries in 1821, in the "Systema mycologicum," 2: 324, was the first to place it under *Cantharellus*, where it seems to belong. Hennings in Engler and Prantl (1897), has followed Karsten in breaking up the old genus *Cantharellus*, as described by Adanson in Juss. Gen. p. 6 (1789) and places this genus under *Leptotus*.

The fungus has been found several times in Europe and especially in England, as Cooke and Sowerby both record it. The Minnesota collection is the first recorded from America the writer believes. The fungus was found in the early spring, April 1903, by Mr. N. P. B. Nelson. It was growing abundantly upon the coarser mosses, especially species of *Hypnum* in a swamp near the Fish Hatchery, St. Paul.

Cantharellus retirugus is closely related to *C. muscigenus* (Bull.) Fries and *C. lobatus* (Pers.) Fries. It differs from the former in not being truly stipitate, although some specimens show a short pseudostipe. It also is not villose and the veins are strongly anastomosing or reticulate. It differs from *C. lobatus* in being laterally, that is, never centrally attached, and the gills are more truly reticulate than in *C. lobatus*. Again the spores are not spherical or oval but are broadly elliptical.

Cantharellus retirugus (Bull.) Fries.

Pileus to .75 inch in diameter, membranaceous expanded, repand, fan-shaped, margin wavy and lobed darker at edge, near point of attachment, cinereous white to tan or brown at margin; darker beneath, subsessile or expanded into a short flattened stipe-like base at one side, fixed by little fibrils; upper surface minutely scabrous; beneath gills radiating from point of attachment, thin, reticulate and anastomosing; basidia short, simple, two to four

short sterigmata; basidiospores broadly elliptical or pear-shaped, smooth, granulose, 6-10 x 4-8 mic.

On stipe and frond of coarse mosses as *Hypnum* species; England, Kings Cliffe (Cooke), Bear Island (Saccardo); Minnesota (Nelson).

Explanation of Plates.

Plate XI.

Exobasidium mycetophilum (Peck) Burt, natural size.

Plate XII.

Cantharellus retirugus (Bull.) Fries, natural size.

Figure 1. Photographed in nature.

Figure 2. Upper surface, single specimen.

Figure 3. Lower surface, single specimen.

Plate XIII.

Figures 1-9. Exobasidium mycetophilum, magnified 485 dm.

Figure 1. Diagram of cross section of cap of host and parasite.

H = hymenium, S = sterile tissue of parasite, A = host.

Figure 2. Old basidia,

Figure 3. Clump of basidia tips.

Figure 4. Isolated spores.

Figure 5. Diagram of cross section of stipe of host and parasite.

H = hymenium, S = sterile tissue of parasite, A = host, C = cavity of parasite.

Figure 6. Basidia with spores.

Figure 7. Young basidia tip with spores.

Figure 8. Old basidia tip with sterigmata.

Figure 9. Clamp connections.

Figures 10-16. Cantharellus retirugus (Bull.) Fries.

Figure 10, 11. Clamp connections.

Figure 12. Old basidia.

Figure 13. Young basidia with two spores.

Figure 14. Basidia with four spores.

Figure 15. Basidia with spores.

Figure 16. Spores with sterigmata still attached.

PLATE XI

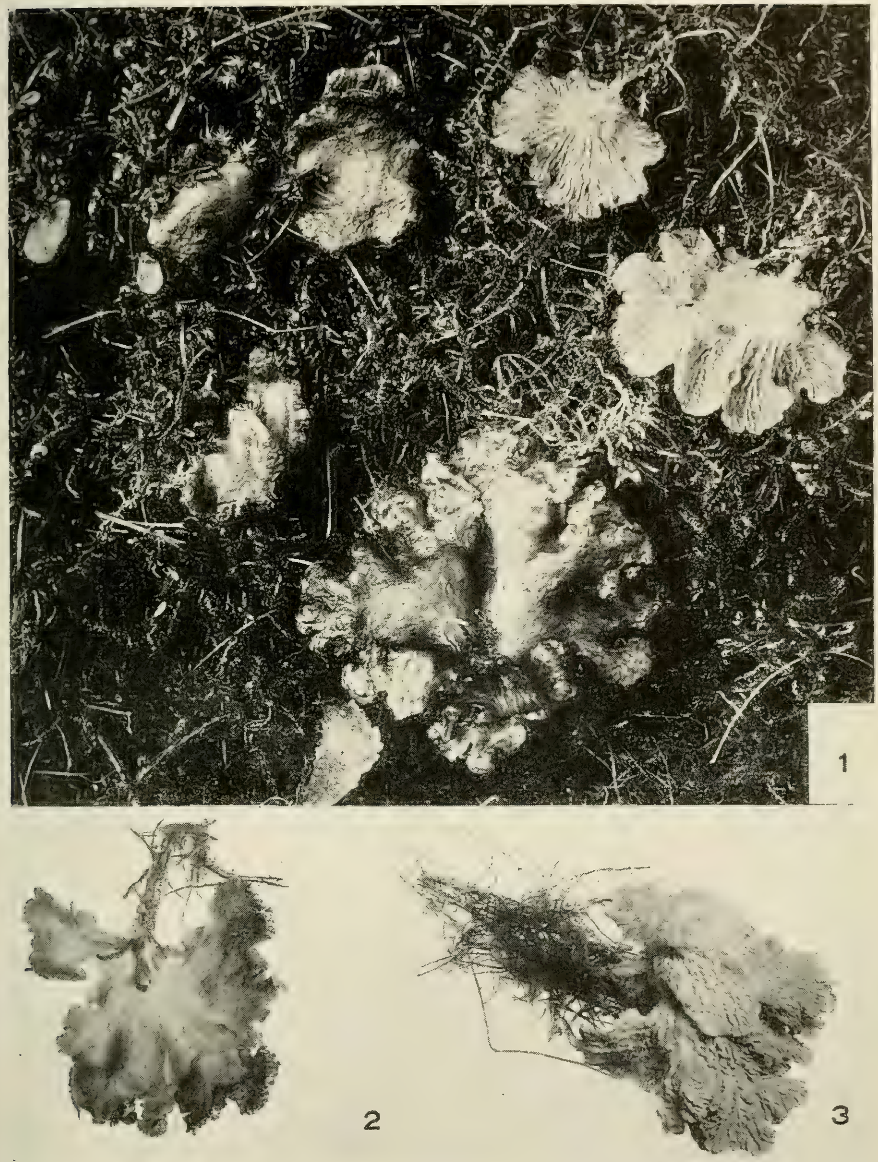

PLATE XII.

PLATE XIII.

HELIOTYPE CO., BOSTON.

5. THE PEZIZALES, PHACIDIALES, AND TUBERALES OF MINNESOTA.

Daisy S. Hone.

The following is a report of the Minnesota Pezizales, Phacidiales, and Tuberales, with the exception of the Ascobolaceae, collected at various times since 1886. In 1876 Dr. A. E. Johnson collected various fungi, and published a list in the Bulletins of the Minnesota Academy of Natural Science during the years 1876-1879. This collection of Dr. Johnson's was not presented to the University and the Minnesota Academy of Science reports that the specimens which Dr. Johnson did retain have now been destroyed. In 1886 Professors J. C. Arthur, L. H. Bailey, and E. W. D. Holway made a collection of fungi in St. Louis County and a list was published in Bulletin No. 3, of the Geological and Natural History Survey of Minnesota (1887). Three new species of the Pezizales were there recorded. The specimens were deposited with the Herbarium of the University of Minnesota and are included in this report. Since that date various collections have been made by Doctors A. P. Anderson, E. P. Sheldon, C. A. Ballard, E. M. Freeman, Prof. F. K. Butters, the writer and others.

This report is a continuation of the work of which "Minnesota Helvellineae," published in Minnesota Botanical Studies, Vol. III. Part 3. p. 309, 1904 was a part. The work was undertaken in the fall of 1902 at the suggestion of Dr. E. M. Freeman and Professor Conway MacMillan, then State Botanist. A large part of the work was done under the direction of Dr. E. M. Freeman to whom I wish to acknowledge my indebtedness for his untiring and valuable advice and supervision.

The Classification of Schroeter and Lindau in Engler and Prantl, "Die Natürlichen Pflanzenfamilien," 1: 3: 173. 1894, has been followed with few exceptions. The works of the following authors have been consulted: Rehm in "Rabenhorst's Kryptogamen Flora," Pilze, 1: 3: 1896; Cooke in "Mycographia"; Phillips, Massee, Berke-

ly, Peck, Morgan, and Ellis. All the papers and works listed in the Bibliography have also been consulted. In the synonomy all references not verified are marked with an asterisk.

The descriptions of species are based largely upon the personal observations of the writer made upon the Minnesota material. Previously published descriptions have been used freely but only in so far as they agree with the Minnesota plants. Comparisons have been made with the exsiccati in the University Herbarium and the results noted in each case. Many other exsiccati were also examined but were not noted on account of incomplete specimens or nonagreement with the Minnesota plants. In citing exsiccati, those listed by Dr. Rehm are given first place. Plate references have been cited wherever figures were found to agree with the Minnesota plants. The terminology of Phillips in the "Manual of British Discomycetes" has been in large part followed. All the species described, unless otherwise noted, are now in the collections of the Museum and Herbarium of the University of Minnesota. They are preserved both in a mixture of two per cent formalin and seventy per cent alcohol and also in the dried condition. The photographs were taken by Mr. C. J. Hibbard, formerly on the staff of the Minnesota Geological and Natural History Survey. The data of collections are given in the following order: county, date, collector, and collector's field number.

Since the old genus Peziza has been split up into so large a number of genera by various authors with not even an approach to unanimity in the delineation of the new genera so founded, it has been thought best to adopt Lindau's subgeneric classification as generic. In one instance, however, exception has been made to this rule for reasons noted under the species, viz., *Urnula craterium* (Schwein.) Fr.

In all three orders, seven families, thirty-seven genera, ninety-four species with four varieties are here reported from Minnesota.

For assistance in various ways I am indebted to the following: Professor F. E. Clements, Professor E. W. D. Holway, and Professor F. K. Butters, of the University of Minnesota; Dr. E. J. Durand, of Cornell University; Dr. H. Rehm, of University of Munich; Dr. Bruce Fink, of Miami University; Mr. J. C. Hibbard, of Camera Craft Shop, Minneapolis; Mr. H. S. Jackson, of Delaware College; Dr. R. H. Denniston, of University of Wisconsin; and Professor F. J. Seaver, of North Dakota Agricultural College.

Key to the Orders.

I. Cup inverted, capitate, clavate, or mitrate, stalked, fleshy, waxy, or gelatinous. **Helvellales.**

II. Cup-like, becoming concave or convex, sessile or stalked.

1. Spore surface open early, without firm covering, fleshy or waxy. **Pezizales.**
2. Spore surface inclosed in a firm covering, open at maturity, black. **Phacidiales.**

III. Hypogaeous fungi, subglobose, indehiscent. **Tuberales.**

Key to the Families.

I. Helvellales. (Saddle Fungi.)

1. Capitate; smooth, or folded, or ribbed; fleshy or waxy. **Helvellaceae.**
2. Clavate or mitrate; fleshy or rarely gelatinous. **Geoglossaceae.**

II. Pezizales. (Cup Fungi.)

1. Cups fleshy or waxy, rarely gelatinous; ends of paraphyses free.
   (1) Cups generally large and fleshy; exciple scarcely differentiated. **Pezizaceae.**
   (2) Cups generally small and waxy; exciple distinct.
      a. Cup stalked or substalked; growing upon wood or herbaceous stems. **Helotiaceae.**
      b. Cups sessile; growing upon herbaceous plants. **Mollisiaceae.**
2. Cup leathery or cartilaginous; ends of paraphyses united to form a covering; mainly black.
   A. Cup free from first, never enclosed in a membrane. **Patellariaceae.**
   B. Cup first submerged, later breaking thru the epidermis, often first inclosed in a membrane. **Cenangiaceae.**

Key to the Genera.

Hevellaceae.

A. Cap bell-shaped or lobed, attached to the stem only at central point.
   (1) Cap lobed, wrapped around the stem. **Helvella.**
   (2) Cap bell-shaped, free. **Verpa.**

B. Cap entirely hollow, or only in upper part; cavity of cap in continuation of that of the stem; cap pitted or ribbed. **Morchella.**

Geoglossaceae.

A. Cap sessile on the stem or attached to it.
   (1) Cap spoon-shaped, decurrent on both sides of the stem; spores linear. **Spathularia.**
   (2) Cap clavate, spores two-many-celled.
      (a) Spores brown. **Geoglossum.**
      (b) Spores colorless. **Leptoglossum.**

B. Cap distinguished from the stem by a definite rind, mitrate.
- (1) Spores elongate-elliptic; cap gelatinous. **Leotia.**
- (2) Spores linear; cap not gelatinous. **Cudonia.**

Pezizaceae.

A. Spores spherical.
- (1) Cup externally hairy. **Pseudoplectania.**
- (2) Cup externally not hairy. **Plicariella.**

B. Spores elliptical, obtuse or rarely acute.
- (1) Cup externally hairy. **Lachnea.**
- (2) Cup externally not hairy.
  - (a) Cup regular; margin glabrous.
    - 1. Sap colorless.
      - a. Asci stain blue with iodine.
        - (x) Cup sessile or subsessile, generally large. **Plicaria.**
      - b. Asci do not stain blue with iodine.
        - (x) Spores smooth or rough not reticulate.
          - (m) Cup sessile, generally small. **Humaria.**
          - (n) Cup more or less stalked.
            - x. Stem generally short, even, and glabrous.
              - m. Cup goblet or beaker-shaped. **Geopyxis.**
              - n. Cup becoming more or less flattened. **Discina.**
            - y. Stem uneven, often sulcate. **Acetabula.**
            - z. Stem long, slender, not sulcate, externally rough. **Macropodia.**
        - (y) Spores at last reticulate. **Aleuria.**
    - 2. Sap colored, milky. **Galactinia.**
  - (b) Cup irregular, split or elongate on one side, ear-shaped. **Otidea.**

Helotiaceae.

A. Cup externally hairy.
- (1) Cup fleshy, conspicuous. **Sarcoscypha.**
- (2) Cup waxy or membranous, inconspicuous.
  - (a) Spores spherical or egg-shaped. **Lachnellula.**
  - (b) Spores elliptical or elongate.
    - 1. Cups delicate, stalked. **Dasyscypha.**
    - 2. Cups thick, not stalked. **Lachnella.**

B. Cups externally not hairy.
- (1) Cup fleshy, thick or membranous, mainly conspicuous.
  - (a) Cups arising from an under-ground sclerotium. **Sclerotinia.**
  - (b) Cups not arising from an under-ground sclerotium.
    - 1. Spores at maturity stalked. **Rutstroemia.**
    - 2. Spores at maturity not stalked.
      - a. Substratum colored green. **Chlorosplenium.**
      - b. Substratum not colored green. **Ciboria.**

(2) Cup waxy or tough, mainly inconspicuous.
  (a) Spores spherical. **Pitya.**
  (b) Spores elliptical or fusiform.
    1. Spores at maturity 1-celled.
      a. Cup margin entire. **Hymenoscypha.**
      b. Cup margin toothed. **Cyathicula.**
    2. Spores at maturity 2-4 celled. **Helotium.**
(3) Cup cartilaginous or gelatinous.
    1. Spores at maturity many celled. **Coryne.**

Mollisiaceae.

A. Cup fleshy or waxy, small.
  (1) Cup from first free upon the substratum, seated upon a web of hyphae, spores 1 celled. **Tapesia.**
  (2) Cup at first immersed in the substratum, then erumpent, spores many celled. **Beloniella.**

B. Cup cartilaginous, or subgelatinous, spores 2-4 celled at last. **Calloria.**

Patellariaceae.

A. Cup free, sessile, round; spores 2-celled, becoming brown. **Karschia.**

Cenangiaceae.

A. Cup when fresh leathery, horny, or waxy.
  (1) Stroma not present.
    (a) Spores 1-celled, colorless. **Cenangium.**
    (b) Spores thread-like, many-celled.
      1. Spores colorless **Godronia.**
      2. Spores brownish. **Tryblidaria.**
  (2) Cup seated upon a more or less well developed stroma.
    (a) Spores 8 in ascus, not germinating in ascus. **Dermatea.**
    (b) Spores many, conidia-like, germinating in ascus. **Tympanis.**
  (3) Cup seated upon a hypothallus, not a stroma, not immersed. **Urnula.**

B. Cup when fresh gelatinous, stalked or sessile. **Bulgaria.**

Phacidiaceae.

A. Cup gregarious on a stroma, spores needle-shaped, hyaline. **Rhytisma.**

Eutuberaceae.

A. Spore surface convoluted; asci short sack-like, mostly 4-spored. **Tuber.**

Order Pezizales.

Family I. Pezizaceae.

Mycelium mostly within the substratum; usually saprophytic; cups mainly superficial, fleshy, concave, plane or convex, sessile or stipitate, exterior glabrous or hairy, smooth or rough, exciple and hypothecium of similar structure, composed of loose roundish cells.

1. PSEUDOPLECTANIA FUCKEL.

Cups solitary or caespitose, fleshy, cupulate to saucer-shaped, dark swarthy, base plicate into a short stipe; exterior tomentose; spores globose, smooth, hyaline, continuous.

1. **Pseudoplectania melaena (Fr.) Sacc. Syll. Fung. 8: 165. 1889.**

Peziza melaena Fr. Syst. Myc. 2: 60. 1823.

Solitary or caespitose, stipitate, fleshy, to tough, closed at first becoming hemispherical, expanded saucer-like but not repand, up to 1:5 cm. in diameter; hymenium smooth, grayish-black to brown-black; margin erect, entire or torn; exterior glabrous to tomentose with short thin-walled, blunt, septate, straight, brown hairs; stipe short-cylindrical, plicate into the base of the cup when dried, black, rooting slightly; spores globose, smooth, hyaline, granulate, 9-13 mic. in diameter; paraphyses filiform.

On fallen logs in woods, rare; Lake, June 1893, Sheldon 4508, 4583; St. Louis, June 1903, Sheldon 4429.

Very closely related to *Ps. nigrella* (Pers.) Fuckel, Thümen, Mycoth. Univ. 18, from which it differs only in that it is stalked and does not grow upon the ground. The tomentose character is not so distinct, as some of the specimens are nearly glabrous and the margin has no fringe of hairs.

Plates: Rehm, Raben. Krypt. Fl. 1: 3: 1030. fig. 1; Cooke, Mycogr. pl. 49. fig. 193. Alb. & Schw. Consp. fung. Nisk. pl. 5. fig. 2; Boudier, Icones Mycol. 2. pl. 343.

2. PLICARIELLA LINDAU.

Cups gregarious or caespitose or solitary, fleshy, mainly small, sessile, concave to plane; exterior smooth or rough, not hairy; spores globose, smooth or rough, hyaline, continuous.

1. **Plicariella polytrichi (Schum.) Lindau. Engler & Prantl, Nat. Pflanz. 1:2:180. 1897.**

Peziza polytrichi Schum. Enum. Plant. Saell. 1:423. 1801.

Barlaea polytrichi Sacc. Syll. Fung. 8: 113. 1889.

Detonia polytrichina Rehm, Rabh. Kryptofl. 1:3:1269. 1896.

Gregarious, sessile, fleshy, saucer-shaped, -5 mm. in diameter; margin entire, but wavy, smooth, thick; hymenium orange-red; exterior lighter to whitish, pruinose; spores globose, hyaline, smooth, guttulate, 10 mic. in diameter; paraphyses very slender, not clavate, but curved at the apex, and filled with orange granules and oil globules.

On the ground among moss; Becker, Aug. 1901, Freeman 1147; Ramsey, Oct. 1907, Hone 938.

There seems to be great confusion as to what *P. polytrichi* as described by Schumacher, really was. Cooke (48, p. 29.), Gillet (91, p. 50.), Phillips (162, p. 87.), Rehm (178, p. 927.), Lindau (124, p. 180.), describe the spores as globose and smooth. Massee (132, p. 109; 134, p. 371.) describes them as elliptical and finely warted. In Grevillea, Massee gives synonyms and cites exsiccati in the Kew sets. Upon examination of Roumeguère, Fung. Gall. No. 40-45 in the Minnesota Herbarium, the spores prove to be elliptical, acute, finely warted, 20-24 x 10-12 mic., which agrees with Massee's description of *P. polytrichi* Schum. The Minnesota specimens agree with Lindau and Rehm's interpretation of the size and form of the spores as well as of the cup, for *P. polytrichi* Schum.

Plates: Cooke, Mycogr. pl. 13. fig. 50.

2. **Plicariella fulgens (Pers.) Lindau. Engler & Prantl. Nat. Pflanz. 1:2:180. 1897.**

Peziza fulgens Pers. Myc. Europ. 1:241. 1822.

Otidella fulgens Sacc. Syll. Fung. 99. 1889.

Detonia fulgens Rehm, Raben. Krypt. Fl. 1:3:1269. 1896.

Barlaea fulgens Rehm, Raben. Krypt. Fl. 1:3:930. 1896.

Gregarious and caespitose, sessile, fleshy, cups contorted; exterior greenish-black, almost olive green, scurvy, 1 cm. in diameter; hymenium deep reddish-brown when dry; spores globose, smooth, hyaline, granulose, 4-5 mic. in diameter; paraphyses slender, filled with granules.

On gravel ground: Hennepin, Aug. 1903, Minnesota Mycological Society.

The material examined was dried so that the color when fresh could not be determined.

Exsiccati: Thümen, Myco. Univ. 915; Durand, Discom. 1147 (Detonia fulgens (Pers.) Rehm): Plates: Gillet, Discom. franc. pl. 38; Cooke, Mycogr. pl. 53, fig. 3209.

3. **Plicariella modesta (Karst.) Lindau, Engler & Prantl. Nat. Pflanz. 1: 2: 180. 1897.**

Peziza modesta Karst. Myc. Fenn. 1: 64. 1871.

Barlaea modesta Sacc. Syll. Discom. 113. 1889.

Scattered, sessile, fleshy, closed at first soon expanding to saucer-like, up to 2 mm. in diameter; hymenium orange-colored, margin even, erect; exterior glabrous; spores globose nucleate, hyaline, finely echinulate, 16-18 mic. in diameter; paraphyses slender, gradually becoming clavate, straight, septate, up to 4 mic. wide.

On bare damp ground: Ramsey, Oct. 1907, Hone 940.

Exsiccati: Ellis, North Am. Fung. no. 841.

Plates: Cooke, Mycogr. pl. 9. fig. 33.

3. LACHNEA FRIES.

Cups gregarious or caespitose or solitary, fleshy, small or medium, sessile, hemispherical becoming more or less concave, saucer-shaped; margin and exterior covered with hairs; spores elliptical, smooth or rough, hyaline, continuous.

1. **Lachnea hemisphaerica (Wigg.) Gill. Discom. franc. 73. 1879.**

Peziza hemisphaerica Wigg. Flor. Holz. 107. 1780.

Solitary or caespitose, sessile, fleshy, globose then hemispherical, finally quite saucer-like with margin turned back, tough, up to 3.5 cm. in diameter; hymenium bluish-white, smooth; margin often wavy, fringed with rigid, long, pointed, septate, brown setae, very variable; exterior pilose, brown, furnished upward with the brown setae; spores elliptical, obtuse, continuous, hyaline, biguttulate, first smooth becoming verrucose at maturity, 18-25 x 10-14 mic.; paraphyses septate, slightly clavate, straight, up to 8 mic. wide at apex.

On moist ground and decaying wood in shady places: St. Louis, July 1886, Holway 159; Cass, Sept. 1898, Freeman & MacMillan 184; Houston, Aug. 1900, Lyon 740; Hennepin, Sept. 1900, Freeman 774, 841; Wright, May 1900, Freeman 670; Ramsey, Sept. 1900, Freeman 813; Becker, Aug. 1901, Freeman 1085; Cook, Aug. 1903, Freeman & Ballard 111; Hennepin, Sept. 1903, Hone.

Exsiccati: Sydow, Mycoth. March. 4167, 1164, 1464; Ellis, North Am. Fungi 837: Plates: Gill. Discom. franc. pl. 61. fig. 1; Cooke, Mycogr. pl. 30. fig. 115; Pabst, Crypto. Fl. Taf. 19; Boudier, Icones Mycol. 2. Pl. 352.

2. Lachnea gregaria (Rehm) Phill. Brit. Discom. 214. 1887.

Humaria gregaria Rehm, Ascom. Exs. 6. 1869.

Humaria (*Peziza*) *gregaria* Rehm, Ascom. no. 6. Winter, Flora. 508. 1872.

Sarcoscypha gregaria Cooke, Mycogr. 69. pl. 32. fig. 123. 1879.

Gregarious, sessile, first globose then hemispherical to expanded, fleshy, up to 2 mm. in diameter; margin involute, fringed with long, brown, septate, slender, thick walled, tapering setae; exterior brownish; hymenium greyish, even; spores elongate elliptical, slightly acute, hyaline, mainly guttulate, verrucose, continuous, 18-20 x 9-10 mic.; paraphyses slender, septate, very slightly clavate.

On ground: Washington, Sept. 1907, Hone 847.

Growing as this species does with *L. hemisphaerica* Gill., it seems very much like a miniature form of the latter, but the spores are strongly verrucose and acute as Cooke figures them. The specimens differ from *L. albo-spadicea* in slightly smaller and strongly verrucose spores. Both species mentioned grow in company with *L. hemisphaerica* and may easily be mistaken for miniature forms of it.

Exsiccati: Thümen, Myc. Uni. 2209 (*Humaria gregaria* Rehm); Krieger, Fungi. sax. 1628. The spores agree in size and shape but are smooth, while the Minnesota material has beautifully verrucose spores. The former are undoubtedly young stages: Plates: Cooke, Mycogr. pl. 32. fig. 123.

3. Lachnea rubra Phill. Brit. Discom. 225. 1887.

Peziza theleboloides var. *rubra* Cooke, Fung. Brit. ser. I. no. 572. Grev. 3. fig. 119. 1874.

Peziza rubra Cooke, Mycogr. pl. 30. fig. 152. 1879.

Single or gregarious, fleshy, sessile, subglobose and closed when young, becoming expanded with margin elevated, up to 3 mm. in diameter; margin entire; exterior and margin sparingly covered with short smooth, brown, thick-walled, 2-4 septate tapering setae, 10 mic. wide; spores broadly elliptical, obtuse, smooth, hyaline, continuous, eguttulate, coarsely granulate, 16-18 x 10-12 mic.; paraphyses clavate, 10-12 mic. wide.

On decaying grass stems in water in laboratory: Hennepin, Dec., Jan., Feb. 1907-08, Hone 1005.

This is not the same as *Peziza rubra* Peck which seems to be a true *Humaria* according to Cooke, Mycogr. 31.

4. Lachnea scutellata (L.) Gill. Discom. franc. 75. 1879.

Peziza scutellata Linné, Spec. Plant. 1: 1181. 1753.

Usually gregarious, sessile, fleshy, subglobose and closed at first, becoming disk-like and plane, attached by a central point, 2 mm. to 1 cm. diameter; hymenium bright-scarlet to vermilion-red, smooth; margin fringed with long brown setae; setae thick-walled, septate, pointed, brown, over 260 mic. long; exterior is lighter colored and villose with short brown setae; spores elliptical, obtuse, continuous, hyaline, first smooth, becoming reticulate, not verrucose at maturity, eguttulate generally but coarsely granulate, 16-24 x 10-14 mic. in diameter; paraphyses septate, clavate, apex filled with orange-red granules, 8 mic. wide.

On rotten stumps, sticks, bark, etc., in very damp regions, especially on wood on the ground among moss in swampy places. Very common and abundant. May-Sept. 1876, Johnson 551 (not preserved); St. Louis, July 1886, Holway 149; Hennepin, June 1890, Sheldon 11; Ramsey, July 1893, Sheldon 5457; Cass, Sept. 1898, Freeman & MacMillan 185; Wright, May 1900, Freeman 645; Cook, Aug. 1903, Freeman & Ballard 65; Hennepin, Sept. 1904, Hone 775; Chisago, Sept. 1904, Hone 472; Hennepin, Oct. 1906, Rosendahl; Washington, Oct. 1908, Hone 2003.

Exsiccati: Ellis, North American Fungi. 1310: Plates: Sowerby Eng. Fung. 1. pl. 24; Cooke, Mycogr. pl. 34. fig. 131; Pabst, Crypto. Fl. Taf. 19; Boudier, Icones Mycol. 2. Pl. 368.

5. Lachnea setosa (Nees) Phill. Man. Brit. Discom. 406. 1887.

Peziza setosa Nees, Syst. Pilze. 260. f. 275. 1816.

Gregarious, sessile, fleshy, subglobose and closed when young, becoming saucer-shaped, 1-4 mm. diameter; hymenium orange-red, never vermilion-red, even; margin rolled in, fringed with erect, septate, thick-walled, pointed, brown setae, when dry setae turn in and form a dense erect cluster; exterior pilose with shorter brown setae; spores elliptical, obtuse, continuous, hyaline, first smooth becoming finely reticulate at maturity, eguttulate, 16-20 x 8-10 mic.; paraphyses septate, slightly clavate, containing orange-red granules.

On rotten logs and wood in moist woods. Common and abundant: Hennepin, Sept. 1898, Freeman 243; Ramsey, May 1899,

Freeman 330; Becker, Aug. 1901, Freeman 1054; Hennepin, Sept. 1903, Hone; Hennepin, May 1904, Hone 354; Chisago, Sept. 1904, Hone 471; Washington, Sept. 1907, Hone 839.

Distinguished from *Lachnea scutellata* Gill. by the orange-red, (never vermilion-red) hymenium, by the slightly smaller size, and erect setae, which are most characteristic in a dried state, and by slightly smaller spores.

Exsiccati: Thümen, Fungi Austr. 1013: Plates: Nees, Syst. Pilze. Taf. 37. fig. 275; Cooke, Mycogr. pl. 34. fig. 133.

6. **Lachnea scubalonta (C. et Ger.) Sacc. Syll. Fung. 8: 179. 1889.**

Peziza scubalonta C. et Ger. Grevillea 4: 92. 1875.

Sarcoscypha scubalonta Cooke, Mycogr. 82. pl. 38. fig. 150. 1879.

Gregarious or scattered, sessile, hemispherical and closed, becoming expanded, clinging close to substratum, fleshy, up to 10 mm. diameter; hymenium watery orange-yellow, younger stages tinged with yellow or white; margin erect, thin, fringed with thick-walled, tapering, septate, dark brown setae; exterior covered with the brown setae which become longer upwards, forming long cilia at the margin; spores elliptical, obtuse, smooth, hyaline, continuous, eguttulate or one large central guttula, 12-16 x 6-8 mic.; paraphyses filiform, septate, slightly clavate, 3 mic. at the apex, filled with orange granules.

On cow or moose dung on the ground: Cook, Aug. 1903, Freeman & Ballard 125, 126, 127.

Very closely related to *Lachnea coprinaria* Cke., differing in smaller external cells, slightly smaller spores and very slightly clavate paraphyses with more villose external character. Setae are not confined to the margin as in *L. coprinaria* Cke. and are not stellate as in *Peziza stercorea* Pers.

Plates: Cooke, Mycogr. pl. 38. fig. 150.

4. PLICARIA FUCKEL.

Cups gregarious or caespitose or solitary, fleshy, mainly large, sessile or subsessile, concave to convex, regular or irregular; exterior smooth or rough, not hairy; spores elliptical, smooth or rough, hyaline, continuous.

1. **Plicaria adae (Sadler) Rehm, Raben. Krypt. Fl. 1: 3: 1004. 1896.**

Peziza adae Sadler, Trans. Bot. Soc. Edinburg. 45. 1857.

Peziza (*Cochleata*) *adae* Cooke, Mycogr. 207. fig. 349. 1879.

Subcaespitose, sessile, first globose becoming saucer-shaped and

repand, irregular, thin, delicate, 1-3 cm. diameter; hymenium even, lavender; margin entire, wavy or lobed; spores elliptical, very obtuse, smooth, hyaline, 2 small guttulae, 12-14 x 6-7 mic.; paraphyses filiform not clavate, up to 2 mic. wide, straight.

On damp rotten wood: Crow Wing, July 1904, Hone 419.

This is very variable in form and delicate in texture and color, which is a beautiful lavender.

Plates: Cooke, Mycogr. pl. 97. fig. 349; Cooke, Grevillea 7: 75. pl. 97. fig. 1.

2. **Plicaria repanda (Wahlenbg.) Rehm, Raben. Krypt. Fl. 1:3:1007. 1896. (Plate II.)**

Peziza repanda Wahlenbg. Flora Suecica. Upsaliae. 466. 1824-1826.

Discina repanda Sacc. Syll. Fung. 8: 100. 1889.

Gregarious, caespitose or scattered, subsessile, contracted and folded at point of attachment into short, plicate, stout stipe-like base, often rooting, waxy-fleshy, brittle, first hemispherical, almost closed, becoming saucer-shaped and finely flattened; margin often repand, split, wavy, somewhat crenuate; hymenium watery to light brown, becoming dark brown with age, wrinkled, up to 4.5 inches in diameter; exterior lighter brown to white, farinaceous tc pruinose; spores elliptical, obtuse, hyaline, smooth, continuous, eguttulate or 2 small guttulae, 14-18 x 8-9 mic.; paraphyses filiform, septate, to 3 mic. wide at apex, scarce.

Growing on rotten wood and water soaked logs of maple, birch, etc. June 1876, Johnson 545 (not preserved); St. Louis, July 1886, Holway 258; Chisago, June 1899, Freeman 443; Wright, May and June 1900, Freeman 6-20, 683; Hennepin, Oct. 1900, Butters 56, 57; Becker, Aug. 1901, Freeman 1055; Becker, Aug. 1902, Freeman; Hennepin, May 1903, Hone; Cook, Aug. 1903, Freeman & Ballard 74; Hennepin, May 1904, Hibbard 66; Hennepin, May 1904, Hone 351, 1906, 804.

Exsiccati: Sydow. Mycoth. March. 572: Plates: Cooke, Mycogr. pl. 62. fig. 240; Greville, Scott. Crypto. Fl. 1. pl. 59.

3. **Plicaria muralis (Sow.) Rehm, Raben. Krypt. Fl. 1:3:1006. 1896.**

Peziza muralis Sow., Eng. Fung. tab. 251. 1803.

Geopyxis muralis Sacc. Syll. Fung. 8: 72. 1889.

Peziza varia (Hedw.) Fr. Bresadola, Fung. Tri. 2: 75. 1892.

Gregarious or single, shortly stipitate, first cupulate becoming convex and then concave, revolute to repand, finally very brittle,

up to 4 cm. in diameter when mature; margin torn and repand; hymenium smooth when young, becoming pitted slightly with age, tan to brown; exterior subpruinose or pruinose, white; stipe white, slightly sulcate, 5-6 mm. long; spores broadly elliptical, blunt, hyaline, thick-walled with yellow tinge, eguttulate, very finely granulate, smooth, numerous, 12-14 x 8-9 mic.; paraphyses septate, slightly constricted at septations, clavate, branched, up to 6 mic. wide at apex.

Growing on street sweepings in boxes of Narcissus in green house: Hennepin, Feb.-Mar. 1908, Hone 1009.

The asci of the Minnesota specimens stain blue with iodine while the peculiar constricted character of the paraphyses which Bresadola (35. p. 75. pl. 188.) describes and figures agrees perfectly. The specimens were not found growing upon crevices in a wall as usually given for *P. muralis* (Sow.) Rehm, but in dust and street sweepings in a box. Bresadola has placed the two species *P. muralis* Sow. and *P. varia* Fr. under the same species, where they undoubtedly belong.

Plates: Bresadola. Fung. Tri. pl. 188. 1892.

4. **Plicaria catinoides (Fck.) Rehm, Raben. Krypt. Fl. 1:3:1005. 1896.**

Peziza catinoides Fckl. Fun. Rhen. 1879.

Pustularia catinoides Fckl. Symb. Myc. 328. 1869.

Geopyxis catinoides Sacc. Syll. Fung. 8: 71. 1889.

Single, stipitate, cupulate later margin turned back, whole white to dirty tan, brittle, up to 2-3 cm. in diameter; margin very thin and crenate, disappearing; hymenium smooth; stipe short, 4 mm. long, 2 mm. thick; exterior pruinose; spores broadly elliptical, blunt, hyaline, thick-walled, smooth, eguttulate, 12-14 x 6-8 mic., very numerous; paraphyses filiform very slightly enlarged at apex.

Growing on street sweepings in boxes of Narcissus in company with *Plicaria muralis* (Sow.) Rehm in green house. Hennepin, Mar. 1908, Hone 1008.

Differs from *Plicaria muralis* (Sow.) Rehm in structure of excipulum and hypothecium being much thinner, also truly cupulate, not turning back; hymenium and exterior are of same color, and paraphyses are filiform.

5. **Plicaria vesiculosa (Bull.) Lindau, Engler & Prantl. Nat. Pflanz. 1:2:184. 1897.**

Peziza vesiculosa Bull. Champ. Franc. 270. t. 457. fig. 1. 1791.

Pustularia vesiculosa Fckl. Symb. Myc. 329. 1869.

Pustularia vesiculosa Rehm, Raben. Krypt. Fl. 1: 3: 1017. 1896.

Solitary or gregarious, sessile, very thick, fleshy, globose, expanding to cup-like, campanulate, large, up to 4 or 7 cm. diameter; margin repand but incurved, somewhat notched; hymenium light brown, uneven from basal foldings; exterior coarsely granular, forming large irregular scales, often blistered; base very thick and excipulum often separating from the fleshy thick hypothecium; spores elliptical, obtuse, smooth, hyaline, eguttulate, 18-20 x 12 mic.; paraphyses branched, septate, filiform.

On the ground. Abundant on moist clay in green-house and on manure heap: Hennepin, Oct. 1899, Minnesota Mycological Society; Hennepin, Jan. 1907, Hone; Hennepin, Sept.-Nov. 1907, Hone 820; Hennepin, June 1908, Hone 1010.

Exsiccati: Sydow, Mycoth. March. 2864; Saccardo, Mycoth. Italica 331: Plates: Cooke, Mycogr. pl. 63. fig. 242; Grev. Scott. Crypt. Fl. 2. pl. 107; Sow. Eng. Fung. 1. pl. 4; Rehm, Raben. Krypt. Fl. 1:3:992. fig. 1-4; Boudier, Icones Mycol. 2. pl. 257.

6. Plicaria vesiculosa cerea (Sow.)

Peziza cerea Sow. Eng. Fung. 1. pl. 3. 1757.

Plicaria cerea Fckl. Symb. Myc. 327. 1869.

Pustularia vesiculosa cerea Rehm, Raben. Krypt. Fl. 1:3:1018. 1896.

Gregarious or caespitose, very much contorted by mutual pressure, globose, expanding to cup-like, sessile, fragile, brittle, base plicated into almost a stipe, up to 3.5 cm. diameter; 3 cm. high; margin remains incurved, never repand, wavy, sometimes notched; hymenium yellowish-brown, smooth; exterior whitish, coarsely granular; spores elliptical, obtuse, smooth, very thick-walled, eguttulate, continuous, hyaline, 14-18 x 8-9 mic.; paraphyses filiform, septate, slightly thickened at apex, up to 3 mic. wide.

Very abundant upon ashes and manure heap: Hennepin, May 1903, Hibbard; Ramsey, Sept. 1908, Hone 2000.

The specimens differ from *Peziza vesiculosa* Bull. in the fragile texture and smaller spores. The spores run even slightly smaller than is usually described for *Peziza cerea* Sow.

Exsiccati: Sydow, Mycoth. March. 1465; Krieger, Fungi saxon. 1244 (*Pustularia vesiculosa* var. *cerea* (Sow.) Rehm). Plates: Sow. Eng. fung. 1. pl. 3.

7. Plicaria badia (Pers.) Fckl. Symb. Myc. 327. 1869.

Peziza badia Pers. Observ. Myc. 2:78. 1796.

Gregarious or caespitose or solitary, sessile or narrowed into a very short stem like base, first subglobose, becoming expanded cup-like, regular or often very irregular and wavy, 1-3 cm. diameter, 1.25 cm. high; margin slightly serrate or entire, incurved; hymenium even, deep brown; exterior pruinose to granulose, lighter olive-brown; spores elliptical, obtuse, hyaline, continuous, 1-2 large guttulae, verrucose, 14-18 x 8-9 mic.; paraphyses filiform, straight.

On damp ground; June-July, 1876, Johnson 541 (not preserved); Hennepin, Sheldon; Hennepin, Sept. 1905, Hibbard; Ramsey, Oct. 1907, Hone 939.

Peziza atro-vinosa Ger. & Cooke is closely related but differs in having a purple-brown color, while this is distinctly olive-brown. Hone 939 specimens were light tan when young, becoming dark olive-brown when old.

Exsiccati: Sydow, Mycoth. March. 380; Thümen, Mycoth. Univ. 120; Ellis, North American Fungi. 981: Plates: Cooke, Mycogr. pl. 57. fig. 226; Gill. Discom. franc. pl. 42: Boudier, Icones Mycol. 2. Pl. 283.

8. Plicaria atrovinosa (Cooke & Gerard).

Peziza atrovinosa Cooke & Gerard, Bull. Buff. Acad. Sci. 288: 1875.

Caespitose, sessile, fleshy, thick, cup-shaped then expanded to flattened, saucer-like, up to 1.5 inches across; margin entire, wavy, dark; hymenium smooth, deep vinous-brown; exterior glabrous to granular, lighter brown with purple tinge, base sometimes slightly folded; spores elliptical, obtuse, hyaline, continuous, 1-2 guttulae, asperulate, 14-16 x 6-8 mic.; paraphyses filiform, only very slightly clavate up to 4 mic. wide.

On clay ground: Cook, Aug. 1903, Freeman & Ballard 9; Hennepin, Oct. 1906, Minnesota Mycological Society.

This differs from *Peziza badia* Pers. only in color, as it has a decided purple-vinous tinge with the brown, while all available descriptions except those of Massee (134, p. 436.) distinguish *Peziza badia* Pers. by its olive-brown color. *Peziza saniosa* Schrad. is too small to agree with the Minnesota material and Cooke's description (48. p. 299.) does not agree with it at all.

Plates: Cooke, Mycogr. pl. 57. fig. 225.

9. Plicaria pustulata (Hedw.) Fckl. Symb. Myc. 327. 1869.

Octospora pustulata Hedw. Musci. frond. 2: 19. t. 6. f. A. 1789.

Peziza pustulata Pers. Synops. Meth. Fung. 646. 1801.

Solitary or gregarious, sessile, globose becoming expanded cup-like, up to 3 cm. in diameter, 2 cm. high; margin incurved, thick, firm, fleshy, base often plicate or puckered in, but not drawn in to form a pseudostipe; hymenium pale brown, smooth; margin cut and notched, irregular; exterior very scurvy to blistered, lighter colored; spores elliptical, obtuse, finely verrucose, eguttulate, hyaline, 16-18 x 8-10 mic.; paraphyses filiform.

On ground, June, Sheldon.

The specimens having been preserved in alcohol have become a dirty white color all over with the hymenium a slightly darker shade. It differs from *Peziza vesiculosa* and *Peziza isochroa* in the larger rough spores and more scurvy exterior.

Exsiccati: Sydow, Mycoth. March. 1469, 1747: Plates: Batsch. Elench. Fung. Cont. 1. f. 157; Cooke, Mycogr. pl. 77. fig. 298; Rehm, Raben. Krypt. Fl. 1:3:991. fig. 1-4.

5. HUMARIA FRIES.

Cups gregarious or caespitose or solitary, fleshy, mainly small, sessile, concave to subconvex, generally red or yellow; exterior smooth or rough, not hairy; spores elliptical or fusiform, smooth or rough, hyaline, continuous.

1. Humaria humosa (Fr.) Cooke, Mycogr. 17. fig. 25. 1879.

Peziza humosa Fr. Observ. Myc. 309. 1818.

Gregarious, sessile, fleshy, dish-like to disk-like, up to 6 mm. in diameter; margin dark brown, entire; hymenium brick-red, even; exterior dull reddish grey, glabrous; spores elliptical, obtuse, eguttulate, smooth, continuous, hyaline, uniseriate, 16-20 x 10-12 mic.; paraphyses slender, slightly clavate, septate.

On damp sandy clay under red oak tree, bare ground; 1876, Johnson 550 (not preserved); Hennepin, June 1893, Butters 211.

Plates: Cooke, Mycogr. pl. 7. fig. 25; Boudier, Icones Mycol. 2. pl. 391.

2. Humaria jonella (Quel.) Sacc. Syll. Fung. 8:149. 1889.

Peziza jonella Quel. V. Suppl. Bull. Soc. Bot. de France. 24:328. t. 6. f. 4. 1877.

Mainly solitary, sessile, fleshy, urn-shaped, then expanded, up to 7-8 mm. diameter; hymenium lavender to lilac, even; margin finely and irregularly papillate; exterior pubescent, granular, lighter colored; spores elliptical, elongate, acute, smooth, continuous, pluri-guttulate, hyaline, 26-32 x 10-11 mic.; paraphyses

thread-like, branched, numerous, not clavate, up to 4 mic. wide.

On decayed wood on ground; Cook, Aug. 1903, Freeman & Ballard 135.

Plates: Quel. Bull. Soc. Bot. de France, 1877. 24. t. 6. f. 4.

3. Humaria microspora (Berk. & Curt.) Sacc. Syll. Fung. 8: 131. 1889.

Peziza microspora Berk. and Curt. Grev. 3: 150. 1875.

Gregarious and caespitose, sessile or substipitate, fleshy, fragile, very irregular, up to 2.5 cm. across; hymenium smooth, bright orange; exterior pallid, pruinose; stipe obsolete or very short, a mere fibril sometimes; spores elliptical, obtuse, smooth, 1-2 guttulate, 6-8 x 3-4 mic.; paraphyses slender.

On rotten wood near ground and on the ground; Hennepin, Sept. 1900, Freeman 787.

The original description for *Peziza microspora* B. & C. in Grev. 3: 150 omits any reference to size and the Minnesota specimens are larger than those previously described; e. g. Cooke's measurements give only .25 inch. *Peziza epispatica* B. & Br. is very near and agrees in size, but both color and tomentose-pulverulent character disagree.

4. Humaria fuscocarpa (Ellis & Holway) Morgan, Journal. Myc. 8: 189. 1902.

Peziza fuscocarpa (Ellis & Holway) Morgan, Journal. Myc. 8: 189. 1902.

Aleurina fuscocarpa Sacc. Syll. Fung. 16: 739. 1902.

Scattered or gregarious, sessile, orbicular, 3-4 mm. in diameter; margin incurved; hymenium concave, olive-black; exterior pruinose, lighter colored; spores elliptical, obtuse or acute, biguttulate, continuous, smooth, yellow-brown, 8-10 x 4 mic.; paraphyses filiform.

On old rotten logs; St. Louis, July 1886, Holway 194; Dakota, July 1893, Sheldon 5396.

Rehm (178, p. 514.) calls attention to the smooth character of *Peziza fuscocarpa* E. & H., with which the Minnesota material agrees. This species is retained under *Peziza* as originally placed, although Lindau makes no special provision for brown, elliptical-spored forms.

Exsiccati: Ellis and Everhart, North American Fungi. no. 2325; Seaver, Iowa Fungi. 112-b.

5. Humaria applanata (Hedw.) Rehm, Raben. Krypt. Fl. 1: 3: 949. 1896.

Octospora applanata Hedw. Musci. Frond. 2: 13. tab. 5. fig. c. 1789.

Peziza applanata Fries, Syst. Myc. 2:64. 1823.

Gregarious, fleshy, sessile, fixed by a central point, first disk-like, margin elevated, later flattened with margin wavy, edged with irregular brown papillae giving slight appearance of being crenulate, 5 mm. to 2 cm. in diameter; hymenium even rich dark red-brown; exterior finely pulverulent to granular, lighter colored; spores elliptical, very slightly acute, smooth, continuous, hyaline, uniseriate, granulose; 18-20 x 8-10 mic.; paraphyses septate, broadly clavate, up to 10 mic. broad.

On damp ground or decaying sticks; Wright, June 1900, Freeman 679.

Peziza lividula Phill. as described by Cooke (48, p. 161.) differs only in the "lividopurpurea vel fuliginea" color and asperulate spores, while the specimens described above are dark red-brown with smooth spores. The specimen cited below has spores (10-12 x 6-8) smaller than usually given for P. *applanata*, while the spores of the Minnesota specimens run larger than is given. Nevertheless the material seems to be *P. applanata* (Hedw.) Fries.

Exsiccati: Sydow, Mycoth. March. 4054; Plates; Cooke, Mycogr. pl. 71. fig. 272.

6. Humaria oocardii (Kalchbr.) Cooke, Mycogr. 28 pl. 12. fig. 47. 1879.

Peltidium oocardii Kalchbr. Raben. Fung. Europ. no. 521. Hedw. 20:58:216. 1863.

Gregarious or scattered, sessile, fleshy, dingy orange-yellow, waxy-gelatinous, margin entire, glabrous, up to 2 mm. wide; hymenium smooth; exterior granular; spores elliptical, blunt, smooth, continuous, coarsely granulate, eguttulate, 16-18 x 8-10 mic.; paraphyses septate, clavate, numerous.

On rotten water-soaked log; Wright, May 1900, Freeman 646.

The spores do not show any guttulae as is usually described for *P. oocardii* Cooke, but are thick-walled and coarsely granulate. Cooke's figure 47 agrees perfectly.

Plates: Cooke, Mycogr. pl. 12. fig. 47.

7. Humaria olivatra (Ellis & Holway) Sacc. Syll. Fung. 8: 148. 1889. Nat. His.

Peziza olivatra Ellis & Holway, Arthur, Bull. No. 3. Geo. & Nat. His. Sur. Minn. p. 36. 1887.

Carnose, about 2 mm. across, attached by a central point, smooth and blackish outside, with the thin margin lighter; disk concave,

dark olive when dry; asci clavate-cylindrical, 70-75 x 6-7 mm., subsessile. Paraphyses yellowish-brown, about as long as asci, scarcely thickened above: sporidia biseriate, oblong, yellowish-hyaline, rounded at the ends, 6-7 x 1.5-2 mm. The margin, when dry, is more or less undulate, but not strongly incurved.

On old stumps; Wright, July 1886, Holway 269.

8. Humaria tetraspora (Fckl.) Boud. Bull. Soc. Myc. 1: 106. 1885.

Ascobolus tetrasporus Fckl. Hedwigia. 5: 4. tab. 1. fig. 5. 1866.

Scattered, sessile, fleshy, concave to disk-like, expanded, glabrous, up to 2 mm. diameter; hymenium bright red; exterior slightly lighter in color; spores fusiform and attenuated, at the ends blunt, smooth, continuous, hyaline, 18-20 x 8-10 mic. uniseriate, only four spores in each ascus; one large central guttula, or 2 or 3 smaller ones in each; paraphyses slender, clavate, septate.

On the ground; Ramsey, May 1903, E. A. Cuzner.

Closely related to *P. leucoloma*. (Hedw.).

Exsiccati: Sydow, Mycoth. March. 4363: Plates: Gill. Discom. franc. pl. 52. fig. 1; Cooke, Mycogr. pl. 12. fig. 45; Seaver, Discom. Eastern Iowa, pl. 11. fig. 1; Boudier, Icones Mycol. 2. pl. 393.

9. Humaria pertenuis (Cooke).

Peziza tapeina Cooke, Mycogr. 157. fig. 268. 1879.

Peziza pertenuis Sacc. Syll. Fung. 8: 88. 1889.

Slightly gregarious, sessile, fleshy, hemispherical becoming expanded saucer-like; margin erect, incurved, finely crenulate or entire; hymenium slightly darker, 4 mm.-1 cm. diameter; exterior subfarinose, ashy to dirty white; spores elliptical, obtuse, biguttulate, asperulate, hyaline, 14-18 x 8-9 mic.; paraphyses linear or clavate, straight, septate, when clavate, up to 6 mic. wide.

On soil of river bottom; Houston, Aug. 1900, Lyon 708.

Plates: Cooke, Mycogr. pl. 70. fig. 268.

6. GEOPYXIS PERSOON.

Cups gregarious or solitary, fleshy, large, stipitate, beaker-shape or spreading; stipe short, thick, plain; exterior smooth or rough, not hairy; spores elliptical, smooth or rough, hyaline, continuous.

1. Geopyxis colensoi (Berkeley).

Peziza colensoi Berkeley, Hook. Flora Nov. Zeal. 2: 200. tab. 5. f. fig. 5. 1855.

Sarcoscypha colensoi Sacc. Syll. Fung. 8: 157. 1889.

Solitary, stipitate, thin, rather tough, cup funnel-shaped be-

coming expanded and flattened, greyish-white all over, up to 1.5 cm. diameter; margin even, incurved, wavy; hymenium smooth; exterior minutely pruinose to granulose, plicate at base to form a short thick stipe, which is sometimes inflated or discoid at the base; spores narrowly elliptical-fuscoid, acute, hyaline, smooth, sometimes as many as 5 guttulae, 20-30 x 4-6 mic.; paraphyses filiform.

On decaying and dead logs; Becker, Aug. 1901, Freeman 1056.

Cooke (48. p. 61.) states "The tomentose coating is very delicate and inconspicuous." In the formalin material no trace of it can be seen, but the exterior appears simply granulose or pruinose. The specimens are closely related to *Peziza sylvatica* Karst. and *Peziza pallidula* C. & P., differing mainly in the acute elliptical-fuscoid as well as larger spores. This species is also multiguttulate.

Plates: Cooke, Mycogr. pl. 28: fig. 108.

2. **Geopyxis pallidula (Cooke) Sacc. Syll. Fung. 8: 70. 1889.**

Peziza pallidula Cooke & Peck, Buff. Bull. Acad. Sci. 288. 1875.

Solitary, substipitate, fleshy, waxy, cup infundibuliform becoming flattened, up to 1.5 cm. diameter; to 1 cm. high; margin darker, thin, smooth, incurved, wavy; hymenium even, watery-dingy-white; exterior sub-farinose, dingy-white; stipe short, thick, abbreviated; spores elliptical, obtuse, smooth, eguttulate, hyaline, 12-16 x 6-7 mic.; paraphyses slender, clavate.

On water-soaked log; Wright, May 1900, Freeman 652.

Plates: Cooke, Mycogr. pl. 75. fig. 289.

3. **Geopyxis sylvatica (Karst.)**

Peziza sylvatica Karst. Myc. Fenn. 58. 1871.

Gregarious, shortly stipitate or sessile, fleshy, up to 2.5 cm. diameter; 1 cm. high, when young or fresh gray to light yellow, now old or preserved a dark brown all over; exterior pruinose; spores elliptical, obtuse, smooth, eguttulate, 12-14 x 8 mic.; paraphyses septate, clavate.

On log, common; Goodhue, Aug. 1893, Anderson 787.

Related closely to *Peziza micropodes* Pers. (Syn. meth. fung. p. 642.) and *Peziza lepidota* Fr. (Sys. myc. 2: 54.).

Plates: Cooke, Mycogr. pl. 65. fig. 250.

4. **Geopyxis cupularis (L.) Sacc. Syll. Fung. 8: 72. 1889.**

Peziza cupularis Linn. Sp. Pl. 1: 1181. 1753.

Solitary, shortly stipitate, fleshy, cupulate to campanulate, concave, 1.5 cm. in diameter and high; margin erect, thin, irregularly crenulate; hymenium gray with yellow tinge, even; exterior lighter

yellow-gray, coarsely scurvy to scabrous; stipe very short, formed by the plicate base mainly; spores elliptical, obtuse, smooth, hyaline, continuous, biguttulate, uniseriate, 18-20 x 9-11 mic.; paraphyses slender, only slightly clavate.

On ground in damp places and among moss; June 1877, Johnson 548 (not preserved); Cook, Aug. 1903, Freeman & Ballard 154.

Plates: Gill. Discom. franc. pl. 36; Cooke, Mycogr. pl. 74. fig. 286; Boudier, Icones Mycol. 2. pl. 338.

5. **Geopyxis carbonaria (Alb. et Schw.) Sacc. Syll. Fung. 8: 71. 1889.**

Peziza carbonaria Alb. et Schw. Consp. Fung. Nisk. 314. tab. 4. fig. 2. 1805.

Gregarious or solitary, fleshy, stipitate, cupulate to campanulate, concave, 1.25 cm. across. 2 cm. high; margin erect, minutely and irreguarly crenulate, thin, nearly white; hymenium watery-tan brown, even; exterior lighter brown, minutely scurvy; stipe coarsely scurvy, white, slender, length very variable; spores elliptical, slightly acute, mainly eguttulate, smooth, hyaline, continuous; 10-14 x 6-7 mic.; paraphyses very slender and slightly clavate.

Abundant on ground in burned over regions; St. Louis, July 1886, Holway 191; Cook, Aug. 1903, Freeman & Ballard 124.

Field notes or preserved specimens do not show any trace of red in the hymenium which most authors mention. Nevertheless this seems to be P. *carbonaria* Alb. & Schw.

Exsiccati: Krieger, Fungi Sax. 1269; Sydow, Mycoth. March. 774: Plates: Alb. et Schw. Consp. Fung. Nisk. pl. 4. fig. 2; Cooke, Mycogr. pl. 74. fig. 284.

6. **Geopyxis petaloides (Cooke & Phill.) Sacc. Syll. Fung. 8: 67. 1889.**

Peziza petaloides Cooke & Phill. Brit. Discom. 46. 1887.

Solitary, stipitate, fleshy, thin, firm, cupulate to expanded; margin entire or waved, up to 1-3 cm. across when expanded; hymenium purple-brown, rugose, subumbilicate; exterior pruinose to finely verrucose, fuliginous brown, base rugose; stipe up to 4 cm. long, slender, enlarged up into rugose base of cup and tapering, deeply rooting, floccose; spores elliptical, blunt, minutely asperate, granulate, continuous, hyaline, 10-14 x 5-6 mic.; paraphyses slender, slightly clavate.

On ground among chips and leaf-mould in open areas; Hennepin, May 1905, Hone 777.

The specimens were found sunken to the cup in litter of chips and leaf-mould, so that they appeared sessile. The descriptions

given by Massee (134, p. 379), Rehm (178, p. 1073), and Cooke (48, p. 99), for *Peziza radiculata* Sow., all agree with the described specimens except in color. When fresh the specimens were entirely deep brown or purple-brown with no yellow or white tinge. Evidently it is very closely related to *P. radiculata* Sow. Bresadola's figures (35, pl. 184), for *P. radiculata* agree in form, but not in color.

7. DISCINA FRIES.

Cups mainly solitary, fleshy, large, subsessile, cupulate to saucer-shaped, often turned back; exterior coarsely granular; spores elliptical, smooth, hyaline, continuous.

1. Discina venosa reticulata (Grev.) Rehm, Raben. Krypt. Fl. 1:3: 978. 1896. (Plate XVII. Fig. 2.)

Peziza reticulata Grev. Scott. Cryptofl. 3. tab. 156. 1825.

Discina reticulata Sacc. Syll. Fung. 8: 100. 1889.

Solitary, nearly sessile or narrowed into a short, stout, lacunose and plicate stipe, fleshy, brittle, first cupulate to saucer-shaped with margin entire, involute, later margin becomes waved, spread out, but retaining tendency to be involute, 1-3 inches in diameter; hymenium plicate, undulate and unequal with nodules or reticulations, reddish-brown, 1-3 inches across before becoming depressed and flattened; exterior whitish coarsely granulose to farinose; base plicate; spores elliptical, obtuse, hyaline, continuous, granulate, 18-24 x 10-12 mic.; paraphyses rather stout, clavate, septate, branched, granulate.

On the ground in oak woods; Ramsey, May 1903, Harold Cuzner.

Schroeter (195, p. 43), describing the spores of *P. reticulata* Grev. writes "An beiden Enden mit schwachen, verschwindenden Plasmabelag ohne eigentliche Anhangsel." This is not noticeable in the Minnesota material.

Exsiccati: C. Roumeguère, Fungi selecti. 7124: Plates: Grev. Scott. Cryptflo. 3. pl. 156. 1825; Krombholz, Schwamme VIII. pl. 61. fig. 15-22. 1843.

2. Discina venosa (Pers.) Sacc. Syll. Fung. 8: 104. 1889.

Peziza venosa Pers. Syn. Fung. 638. 1801.

Mainly solitary, fleshy, sessile or base slightly contracted into a stem-like base, up to 5 cm. in diameter; cupulate; margin entire, curved in, later becoming waved; hymenium deep rich umber brown, no olive or purple tinge, smooth or sinuous when mature;

exterior whitish, coarsely granulate or verrucose with nodules; base more or less plicate; spores elliptical; smooth, hyaline eguttulate, uniseriate, granulate when mature, 18-20 x 10 mic.; asci do not stain blue with iodine; paraphyses slender, gradually clavate, septate, granulate, brown at apex.

On ground in humus under oak trees; Hennepin, May 1908. Hone 1014.

The Minnesota specimens show asci which are very young and most of the spores immature, but all characters seem to agree with those given for *P. venosa* Pers.

Exsiccati: Saccardo. Mycoth. Ital. 332: Plates: Boud. Icon. Mycol. II. pl. 254; Cooke, Mycogr. pl. 58. fig. 228.

8. ACETABULA FUCKEL.

Cups solitary, fleshy, large, stipitate, cupulate; stipe short, thick, sulcate; exterior minutely scurvy, ribbed with anastomosing veins running up from the stipe; spores elliptical to oval, smooth, hyaline, continuous.

1. **Acetabula vulgaris Fckl. Symb. Myc. 330. 1869.**

Peziza acetabulum Linn. Spec. Plant. 1: 1181. 1753.

Solitary, stipitate, cup-shaped, fleshy, up to 2 cm. in diameter; hymenium umber-brown even; exterior paler to whitish, minutely scurvy; stipe whitish imperfectly hollow, sulcate, with parallel or anastomosing ribs which run up over the exterior of the cup, as branching veins, glabrous, 1 cm. high; spores nearly globose, hyaline, smooth, one large guttula, 12 x 9 mic.; paraphyses straight, slender and clavate.

On ground in leaf-mould in moist woods; Hennepin, Sheldon.

The spores are small for *P. acetabulum* L. but Rehm, Durand and Seaver all pronounced the Minnesota specimens to be *P. acetabulum* L. Kalkbrenner (110, p. 268, pl. 4. fig. 3), describes *P. costata* and figures it with the spores nearly globose. His figures agree perfectly with the Minnesota specimens. Perhaps *P. costata* should be included as a variety of *P. acetabulum* L. in which case the Minnesota specimens as well as some found in St. Croix Co., Wis. (Hone 784), would come under the variety. Rehm considers *P. costata* as identical with *P. acetabulum* L.

Exsiccati: C. Roumeguère, Fungi selecti. 4161 (*Peziza* (*aleuria*) *acetabulum* L. form *sylvatica*.) Plates: Kalkbrenner, Szepesi Gombak. Jegyzeke II. pl. 4. fig. 3; Gill. Disc. Fr. pl. 32. fig. 1;

Rolland, Bull. Soc. Myc. 81. pl. 5. fig. 1. 1887; Sow. Eng. Fung. 1. pl. 59; Krombholz, Schwamme. pl. 61. fig. 23-24.

9. MACROPODIA FUCKEL.

Cups mainly solitary, fleshy, medium, stipitate, concave to cupulate; stipe long, slender, terete; exterior lighter in color, scurvy to furfuraceous; spores elliptical-fusiform or fusiform, smooth or rough, hyaline, continuous.

1. **Macropodia macropus (Pers.) Fckl. Symb. Myc. 331. 1869.** (Plate XIV. Fig. 4.)

Peziza macropus Pers. Observ. Myc. 26. t. 1. f. 23. 1796.

Solitary, stipitate, tough, first subglobose with margin incurved, becoming expanded, margin always remaining erect never drooping Helvella-like, up to 2 cm. or more in diameter; hymenium, even, grayish-brown; margin and exterior of cup and stipe lighter to grayish, scurvy with small irregular nodules, ends of hyphae nearly villose, up to 5 cm. high; spores fusiform and finely warted, verrucose when mature, elliptical and smooth when young, hyaline, continuous, 1-2 large central guttulae, 18-32 x 8-10 mic.; paraphyses septate, clavate, up to 8 mic. wide at apex.

On ground among moss in shady moist woods; June-July, 1876, Johnson 540 (not perserved); Cook, Aug. 1901, MacMillan, Lyon & Brand 157 (not preserved); Washington, July 1905, Hone 785.

Rehm, Durand and Seaver have seen specimens of the collection (Hone 785) and all agree with this determination.

Exsiccati: Sydow, Mycoth. March. 273; Thümen, Mycoth. univ. 1612, 2119; (spores of all three are fusiform, and verrucose, 16-30 x 8-12 mic.) Plates Gill. Discom. Franc. pl. 31. fig. 1; Grev. Scott. Cryptfl. 2. pl. 70; Cooke, Mycogr. pl. 48. fig. 188; Pabst, Cryptfl. taf. 19.

2. **Macropodia subclavipes (Phill. & Ellis) Rehm, Sydow, Ann. Myc. 2: 354. 1904.**

Peziza subclavipes Phill. & Ellis, North American Fungi. Exs. 985. 1882.

Solitary, stipitate, first subglobose, finely open and expanded, saucer-like, tough to fleshy; hymenium even mouse colored, black-gray, 1.5 cm. in diameter; exterior lighter colored, minutely floccu-lose; stipe still lighter almost white, light leather-colored, subverrucose or minutely scabrous, hollow, slightly enlarged towards base, to 2.5 cm. long; spores elliptical, blunt, continuous, smooth, hyaline,

one large central guttula, 16-20 x 8-10 mic.; paraphyses septate, filiform, clavate, apex brownish and up to 6 mic. wide.

On earth in moist woods, often among moss; St. Louis, July 1886, Holway 227; Hennepin, Sept. 1900, Freeman 741; Hennepin, Aug. 1903, Arthur Johnson 100.

Rehm, to whom material was submitted, thinks that the specimen (Johnson 100), may be *Helvella pezizoides* Afzel., but upon careful comparison with the specimen of *Peziza subclavipes* Phill. & Ell. in the Minnesota Herbarium, it is found to agree perfectly. Holway 227 specimens were determined by Durand as *Macropodia macropus subclavipes* Phill. & Ell., Rehm's description (182, 2: 354) gives "stipite cylindrica, 3 mm. lg., 1 mm. lat." while some of the type specimens of Ellis 985 measure in the dry state up to 6 mm. wide. Saccardo (191, 8: 31) gives "stipite cylindrico, 8 x 1 mm." Holway 227 and Johnson 100, show spores of a fusiform shape but no trace of wartiness is discernible while most of the spores are elliptical and blunt. This may be only a young stage of *P. macropus*, but the color is different and the variation of flocculose exterior of cups with the subverrucose stipe is quite evident, while in *P. macropus* there is no such variation.

Exsiccati: Ellis, North American Fungi. 985.

3. **Macropodia fusicarpa (Ger.) Durand, Journ. Myc. 12: 29. 1906.**

Peziza fusicarpa Gerard, Bull. Torr. Bot. Cl. 4: 64. 1873.

Macropodia pubia Sacc. Syll. Fung. 8: 150. 1889.

Lachnea fusicarpa Sacc. Syll. Fung. 8: 172. 1889.

Solitary or gregarious, sessile or stipitate, first closed becoming cupulate to slightly saucer-like, fleshy, up to 2.5 cm. across; margin slightly incurved; hymenium varying from tan to very dark brown depending upon the age, smooth; exterior slightly darker furfuraceous to velvety with short, brown, septate, blunt setae; spores fusiform, hyaline, continuous, biguttulate, at maturity distinctly verrucose, 32-34 x 9-10 mic.; paraphyses slender only very slightly clavate.

On damp soil and humus, banks of ravines; Washington, Sept. 1907, Hone 845.

The specimens described here grew very abundantly in several places within the radius of a half mile. Although the spores may be slightly small for *Peziza fusicarpa* Ger. they agree better than they do with those of *Peziza semitosta*, its nearest ally.

Exsiccati: Ellis, North Am. Fung. no. 1269; Ellis & Everhart, Fung., Columb., no. 1307 (*Peziza pubia* B. & C.). Plates: Cooke, Mycogr. pl. 28. fig. 110. pl. 29. fig. 113; Seaver, Bull. Lab. Nat. Hist. Iowa. 5. pl. 20. fig. 1.

10. ALEURIA FUCKEL.

Cups gregarious or solitary, fleshy, small or large, sessile or subsessile, concave to cupulate, regular or irregular, some shade of red; exterior lighter colored, rough; spores elliptical, strongly reticulate at maturity, hyaline, continuous.

1. Aleuria wisconsinensis Rehm, Ann. Mycol. 2: 34. 1904.

Gregarious or single, fleshy, saucer-shaped to plate-like; margin erect, entire, smooth almost regular; hymenium smooth, red, up to 1 cm. in diameter; exterior glabrous, white, inconspicuous; spores elliptical, obtuse or slightly acute, reticulate often with an irregular apical papilla, hyaline, uniseriate, eguttulate, 14-16 x 8-9 mic.; paraphyses septate, filiform with globose apex, up to 6 mic. wide at the apex, filled with red granules.

On clay earth lodged in the crevices of an up-turned stump; Hennepin, Oct. 1908, Hone 2004.

The Minnesota specimens differ from *Aleuria bicucullata* Boud. its nearest ally, only in being of a more red color and the spores being reticulate instead of verrucose. The spores agree with those of *P. aurantia* Mull. from which it is separated by its smaller size, different habitat, and distinctly globose paraphyses.

2. Aleuria rutilans (Fries) Gill. Discom. Franc. 53. 1879.

Peziza rutilans Fr. Syst. Myc. 2: 68. 1823.

Humaria rutilans Sacc. Syll. Fung. 8: 133. 1889.

Gregarious or sessile, or stipitate, subglobose becoming expanded and plane, fleshy, from 1 cm.-5 mm. in diameter; margin entire, raised or drooping; hymenium orange to scarlet colored; exterior paler in color, minutely downy but never truly-villose, hairs short, simple, white; spores elliptical, slightly acute, continuous, hyaline, uniseriate, generally one large central oil globule, sometimes two, becoming minutely reticulate, but never warted, 18-22 x 9-11 mic.; paraphyses septate, slender, apex gradually clavate, containing orange granules.

On the ground among and on moss; Hennepin, Nov. 1903, C. Leavitt; Isanti, July 1907, Hone 830; Hennepin, Oct. 1907, Hone 954.

Cooke (48, pl. 15. fig. 57), and Rehm (178, p. 918. fig. 1-4), figure the spores of *P. rutilans* Fr. as verrucose or warty. Massee (132, p. 107, 134, p. 406) figures them as reticulate from specimens named by Fries. Seaver (202, p. 38. pl. 8) calls attention to the reticulate character and places the species under *Aleuria* as Gillet had done, following Engler and Prantl (p. 187) who characterize the subgenus *Aleuria* by the net-like reticulate spores. The Minnesota material is distinctly reticulate.

Exsiccati: Sydow, Mycoth. March. 277 (*Peziza vivida,* spores measure 20-22 x 10-12 mic.) 881; Thümen, Mycoth. uni. 522; Plates: Massee. Grevillea 22: 107; Seaver, Discom. Eastern Iowa. pl. 8. fig. 2.

3. **Aleuria aurantia (Mull.) Fckl. Symb. Myc. 325. 1869.**

Peziza aurantia Muller. Flor. Dan. tab. 67. fig. 2. 1775.

Caespitose and irregular or solitary and quite regular, subsessile or sessile, fleshy, up to 4.5 cm. in diameter; hymenium orange, even or folded by pressure; exterior pinkish to whitish sub-pruinose; spores elliptical, with 2 large guttulae, uniseriate, hyaline, continuous, becoming strongly reticulate when mature, some apiculate, with an apical papilla, 15-18 x 8-9 mic.; paraphyses slender, septate, clavate, apex 8 mic. wide, filled with orange granules.

Growing amid moss on the ground, often near stumps; June 1876, Johnson 542 (not preserved); Hennepin, Sept.-Oct. 1907, Hone 853, 985.

This is one of our most beautiful fall fungi. It has been found in clusters measuring over 4 inches in diameter. A single plant often measuring 1.75 inches. The color is of the brightest orange set off by the deep green of the moss, as it is always found growing amid species of *Polytrichum*. The spore markings, especially the apical papillae, as figured by Rehm and Boudier are strongly developed.

Exsiccati: Thümen. Fungi austr. 928. (spores agree in markings but run slightly larger); Krieger, Fungi sax. 145: Ellis, North American Fungi. 836. Plates: Nees, Syst. Pilze, pl. 37. fig. 279; Cooke, Mycogr. pl. 52. fig. 203; Seaver, Discom. Eastern Iowa. pl. 8. fig. 1; Boudier, Icones Mycol. 2. pl. 313; Rehm, Raben. Krypt. Fl. I: 920. fig. I.

11. GALACTINIA COOKE.

Cups caespitose or solitary, large, fleshy, sessile, hemispherical be-

coming cup-shaped; exterior rough not hairy; spores elliptical, verrucose, hyaline, continuous; when broken a milky sap is exuded.

1. Galactinia succosa (Berk.) Sacc. Consp. Discom. 215. 1884.

Peziza succosa Berk. Ann. & Mag. Nat. Hist. 6: 358. t. 10. f. 5. 1841.

Plicaria succosa Rehm, Raben. Krypt. Fl. 1: 3: 1016. 1896.

Solitary, sessile, waxy, fleshy, hemispherical becoming cup-shaped or cochleate, margin incurved at first becoming erect, generally entire; hymenium up to 2 cm. in diameter, mouse-colored, even, exterior paler in color, dirty-white and delicately scurvy to pruinose; spores elliptical, obtuse, verrucose, biguttulate, hyaline, 16-18 x 8-11 mic.; paraphyses filiform gradually enlarged to 5 mic. at apex.

On the ground in moist woods; Hennepin, Sept. 1900, Freeman 851.

The formalin specimens do not show the yellow juice which is described for *P. succosa* Berk. in a fresh state.

Exsiccati: Thümen, Mycoth. univ. 1411 (*Otidea succosa* Thüm.) Roumeguère, Fungi Selecti. 5335 (*Galactinia succosa* Sacc.). Plates: Cooke, Mycogr. pl. 63. fig. 243; Boudier, Icones Mycol. 2. pl. 284.

2. Galactinia sarazini Boud. Bull. Soc. Myc. France. 3: 147. 1887.

Caespitose, sessile, plicate and folded at the base, some contorted others hemispherical becoming expanded to cup-like and occasionally repand, up to 2.5 inches across, to 1.75 inches high; hymenium brown, very much folded, dark; exterior pruinose to farinose almost white to gray at plicate base growing dark upwards until margin is as dark as the hymenium; margin entire, wavy, often crenate; spores elliptical, obtuse, hyaline, verrucose, some having a short, broad papilla at each end, biguttulate, 10-12 x 4-6 mic.; paraphyses slender, clavate, apex colorless, granulate, 4-6 mic. wide.

On burned-over ground; Hennepin, July 1900, Hibbard.

Near allies of the Minnesota specimens are *Peziza warnei* Peck (146, p. 59), which disagrees in habit and shape of the papillae at the end of the spores; *Discina leucoxantha* Bresadola (35, p. 42), which disagrees in greater size of the spores and color of the fungus. The material described is wholly brown and gray to white with no yellow shades. *Peziza echinospora* Karst. (113, p. 54.) Cooke 48, p. 247) and *Peziza emileia* Cooke (48, f. 379), are also near relatives differing in color and larger spores. Roumeguère, Fungi Gallici, 3453 (*P. emileia* Cke.), shows spores of exactly the same

character and size, except that the verrucose markings are not so prominent.

Plates: Boudier, Bull. Soc. Myc. France. 3: 147, pl. 14. fig. 2.

12. OTIDEA PERSOON.

Cups gregarious or caespitose or solitary, fleshy, large, elongated on one side or split on one side to the base, more or less stipitate; exterior rough; spores elliptical, smooth, hyaline, continuous.

1. Otidea leporina (Batsch.) Fckl. Symb. Myc. 329. 1869.

Peziza leporina Batsch. Elench. fung. 117. 1783.

Peziza uncisa Peck, Report no. 24: 81. 1874.

Gregarious and caespitose, substipitate, fleshy, tough, obliquely cup or ear-shaped, up to 4 cm. high and 2-4 cm. wide; margin wavy, thin rolled in and cut on one side to the base; hymenium smooth, deep brown in preserved state; exterior deep brown, farinose, at base slightly venose costate; stipe thick, short, lacunose, farinose, hollow, cavity opening into hymenium; spores elliptical, obtuse, smooth, hyaline, continuous, biguttulate, 10-14 x 6-7 mic.; paraphyses filiform, not clavate, curved distinctly, tips granulated, 3-4 mic. wide.

On ground in woods; Sept.-Oct. 1876, Johnson 552 (*Peziza uncisa* Peck, not preserved); Cass, Sept. 1898, MacMillan.

The specimens, having been preserved in formalin, show no rusty or ferruginous color, but are a deep almost olive-brown. Character of spores and paraphyses with the size and general habitat all agree with that given for *O. leporina* (Batsch.) Fckl. The species is distinguished from *O. auricula* Cooke by the smaller spores and curved paraphyses.

Exsiccati: Saccardo, Myc. Ital. 512; Roumeguère, Fungi Gallici. 2951; Plates: Schaeff. Icon. Fung. tab. 156 (in part); Cooke, Mycogr. pl. 54. fig. 211; Bresadola Fungi Trident. 2. pl. 182.

2. Otidea cochleata (L.) Fckl. Symb. Myc. 329. 1869.

Peziza cochleata Linn. Spec. Plant. 1: 1181. 1753.

Caespitose, variously contorted and plicate, sessile, fleshy, rather watery to waxy, first globose then expanded spreading and irregularly plicate to repand with margin involute, up to 4 cm. across; hymenium fulvous to deep brown; exterior dingy ochraceous to white, pruinose; spores elliptical, obtuse, smooth, hyaline, continuous, usually biguttulate, 17-21 x 8-10 mic.; paraphyses abundant, long, filiform, clavate, septate, often curved.

On the ground; Ramsey, Sept. 1896, Freeman 234.

The plicate caespitose character as well as watery to gelatinous, loose weft distinguish this from the other species.

Exsiccati: Roumeguère, Fungi selecti. 6371: Plates: Cooke, Mycogr. pl. 54. fig. 212; Gill. Discom. Franc. pl. 40; Sow. Eng. Fung. 1. pl. 5.

3. **Otidea plebophora (B. & Br.) Phillips, Man. Brit. Discom. 55. 1887.**

Peziza plebophora B. & Br. Brit. Fung. no. 1153. Ann. & Mag. Nat. Hist. 1886.

Solitary, substipitate, narrowed to very short stem-like base, shallow cup-shaped, oblique, wavy, thin, waxy, buff all over, 2-3 cm. wide and 2 cm. high; margin entire, wavy; hymenium smooth, sometimes slightly venose; exterior scurvy, slightly rugulose with small veins running up from the base; stipe short thick, to 2 mm. high and thick; spores elliptical, blunt, smooth, hyaline, continuous, biguttulate, 10-12 x 4-6 mic.; paraphyses septate, clavate to globose at apex, 4-6 mic. wide, straight or only slightly blunt.

On sticks buried in the ground; Hennepin, Sept. 1900, Freeman 854.

The venose character is not as strongly marked as in Cooke's figure 217. Lighter color and paraphyses separate this from *O. leporina*.

Family II. Helotiaceae.

Mycelium partially or wholly superficial or within the substratum; saprophytic or parasitic; cups superficial, fleshy-waxy, waxy-membranous, cartilaginous or gelatinous, concave or plane, sessile or stipitate, exterior glabrous or hairy, hypothecium differentiated from the exciple which is composed of elongate, thin-walled, bright-colored cells.

1. SARCOSCYPHA FRIES.

Cups gregarious or caespitose, fleshy-waxy, stipitate, generally cupulate, usually bright-colored; exterior tomentose and paler than the interior; hairs short or long, white or often appressed and inconspicuous with age; spores elliptical, large, smooth, hyaline, continuous.

1. **Sarcoscypha coccinea (Jacq.) Cooke. Mycogr. 55. fig. 95. 1879.** (Plate XVIII.)

Peziza coccinea Jacq. Miscell. Austr. Bot. t. 169. 1776.

Lachnea austriaca (Beck) Sacc. Syll. Fung. 8: 169. 1889.

Caespitose, gregarious, stipitate or sessile, closed, globose at first becoming shallow cup-shaped, sometimes quite irregular; margin entire, often split; hymenium brilliant scarlet, even, 2-4 cm. in diameter; stipe short, thick when present; exterior white, clothed with dense tomentum, when young of delicate, flexuose, septate hairs, mature specimens lose some of the tomentum; spores elliptical, obtuse, hyaline, smooth, thick-walled, continuous, straight, 24-34 x 8-12 mic.; paraphyses filiform only slightly thickened at the apex and filled with orange granules.

On rotting sticks and branches partially buried in leaf-mould, moist woods; Nov. 1876, Johnson 556 (not preserved); Hennepin, April 1900, Freeman 559; Hennepin, April-May 1901, Freeman 85; Ramsey, April 1901, 1903, Freeman 958; Hennepin, April-May 1905, 1906, Hone 706; Hennepin, Sept. 1900, Freeman 852; Hennepin, Sept.-Oct. 1903, Hone; Hennepin, Oct. 1907, Hone.

Sarcoscypha coccinea (Jacq.) Cooke is very abundant here in the early spring; often the bright scarlet cups appear breaking through the frozen ground even when lightly covered with snow. Late in the fall we find these same scarlet cups, but very seldom if ever do we find mature spores in the fall. The cups are lined with paraphyses filled with scarlet granules and scattered young asci just beginning to form spores. Some of the asci do not show a sign even of spore formation.

Exsiccati: Ellis, North American Fungi. 434; Plates: Grev. Scott. Crypt. 3. pl. 171; Rolland, Bull. Soc. Myc. 77. pl. 1. 1887; Cooke, Mycogr. pl. 25. fig. 95; Gill. Discom. Franc. pl. 58. fig. 1; Sow. Eng. fung. 1. pl. 13.

2. **Sarcoscypha floccosa (Batsch.) Cooke, Mycogr. 56. fig. 97. 1879.**

Peziza floccosa Batsch. Elench. Fung. 223. 1783.

Gregarious or solitary, stipitate, fleshy, funnel-shaped, 8-9 mm. in diameter, 2.5 cm. high; margin incurved, fringed with long white hairs; hymenium bright scarlet, even; exterior white, tomentose, also the long, tapering stipe; stipe gradually expanding into the cup; hairs long, white, numerous; spores fusiform or elliptical, obtuse, very thick-walled, eguttulate, 18-34 x 10-12 mic.; paraphyses filiform, septate, slender.

On ground or on dead, buried sticks, in moist woods; Waseca, June-July, 1891, Sheldon 605, 667; Ramsey, July 1904, Freeman; Crow Wing, July 1904, Hone 419.5.

Spores of Hone No. 419.5 run very large and are of same character as in *S. protracta* (Fries) Sacc., but not as large as the average of this species. The shape of the cup and very tomentose character of the specimens agree with that given for *S. floccosa* Cke. Freeman's specimens contain both acute-fusiform spores and obtuse elliptical in same hymenium, the elliptical ones being smaller. The shape of the cup and tomentose character place it in *S. floccosa* Cke.

Exsiccati: Ellis, North American Fungi. 435; Plates: Cooke, Mycogr. pl. 25. fig. 97.

3. **Sarcoscypha occidentalis (Schw.) Cooke, Mycogr. 55. fig. 96. 1879.**

Peziza occidentalis Schwein. Syn. Fung. 171. no. 781. 1834.

Gregarious or solitary, stipitate, fleshy, cupulate; margin entire, incurved; hymenium bright scarlet, even, to 1 cm. in diameter; exterior paler scarlet to white, almost glabrous, with very short white hairs, small and inconspicuous, sometimes absent altogether; stipe white, tapering, 1-4 cm. long; spores elliptical, obtuse, smooth, hyaline, with 2 medium guttulae, 16-20 x 8-10 mic.; paraphyses filiform, septate.

On dead twigs, buried in the ground; Waseca, June 1891, Sheldon 580; Cook, Aug. 1901, Lyon, Brand & MacMillan 84; Hennepin, June 1903, Butters; Hennepin, June 1904, Lyon 838; Ramsey, July 1904, Freeman.

The specimens were found in one collection, growing with *S. floccosa* Cke. from which it differs in the almost glabrous exterior. The hairs are either inconspicuous or absent. Length of stem depends upon the depth to which the sticks upon which it grows are buried.

On wood on the ground; Cook, Aug. 1903, Freeman & Ballard 42.

Exsiccati: Ellis, North American Fungi, 436; Plates: Cooke, Mycogr. pl. 25. fig. 97.

4. **Sarcoscypha protracta (Fries) Sacc. Syll. Fung. 8: 155. 1889.**

Peziza protracta Fries, Nov. Symb. Mant. 230. 1851.

Solitary, stipitate, pear-like, becoming funnel-shaped and then cupulate; 2.5 cm. high, fleshy, fragile; margin crenulate, incised, thin, erect, or revolute; hymenium even, bright scarlet, to 1 cm. diameter; exterior and stipe white and tomentose; stipe slender, tapering downward; spores fusiform, acute, large, smooth, hyaline, eguttulate, thick-walled, 32-40 x 10-14 mic.; paraphyses scarce, filiform and only very slightly enlarged upward, straight, to 6 mic. at apex.

On the ground; Hennepin, May, 1903, Hibbard.

Separated from *S. floccosa* Schw. by the shape of the cup, shorter hairs, crenulate margin, and immense size of the spores. Demarcation between cup and stipe is very distinct with the cup quite cupulate and the stipe slender. The material does not show the numerous guttulae recorded for the spores of *S. protracta* Sacc. Perhaps they appear only when more mature. *S. protracta* (Fr.) Sacc. seems to be identical with *S. alpina* E. & E. Torr. Bull. Bot. Cl. 24: 281.

Plates: Cooke, Mycogr. pl. 25. fig. 98; Borszcz. Fungi Ingrici. pl. 4. 5; Wettstein, Verh. Zool.-Bot. Ges. 383. t. 16 (?).

5. **Sarcoscypha melastoma (Sow.) Cooke, Mycogr. 59. pl. 27. fig. 103. 1879.**

Peziza melastoma Sow. Eng. Fung. tab. 149. 1797.

Plectania melastoma Fckl. Sacc. Syll. Fung. 8: 163. 1889.

Solitary, sessile or substipitate, fleshy, firm, cup-shaped or irregular, 3 cm. in diameter; margin crenulate or coarsely notched; blackish-brown; hymenium even, smooth, black; exterior, pubescent brown-black, sessile or folded at base to form short plicate point of attachment, rooting by very long, septate, coarse, flexuose, black filaments or hairs, which are 4-6 mic. wide, 2 cm. high; spores elliptical, oblong, rather acute, smooth, hyaline, uniseriate, continuous, eguttulate, granulate, 20-24 x 8-9 mic.; paraphyses numerous, filiform, slender.

2. LACHNELLULA KARSTEN.

Cups gregarious, waxy, minute, substipitate, hemispherical, becoming saucer-shaped; exterior tomentose with white hairs longer toward the margin; spores egg-shaped to globose, smooth, hyaline, continuous.

1. **Lachnellula resinaria (Cke. & Ph.) Rehm, Rabh. Kryptfl. 1: 3: 864. 1896.**

Peziza resinaria Cooke & Phill. Grev. 3: 185. 1874.

Gregarious, stipitate, 0.25-1 mm. high, 0.5 mm. wide, turbinate to expanded; hymenium smooth, orange-yellow; margin incurved, fringed; exterior and short stipe tomentose, hairs longer towards margin forming fringe, white; spores elliptical and very minute, lower ones in ascus smaller than those near apex, smooth, hyaline, continuous, 1.66-2.5 mic. x 2.49-3.5 mic.; paraphyses cylindrical, apex slightly thickened, free at the ends.

On trunk and branches of *Abies balsamea;* Cass, Sept. 1896, A. P. Anderson.

The above description is taken from A. P. Anderson's paper in Bull. Torr. Bot. Cl. 29: 23-34, 1902. The specimens were not deposited in the University herbarium and the writer has therefore not had an opportunity to examine them.

Plates: Anderson, Bull. Torr. Bot. Cl. 29. pl. 1.

3. DASYSCYPHA FUCKEL.

Cups gregarious, fleshy-waxy, minute, stipitate, concave to plane; exterior pilose or villose, hairs short, white or gray; spores elliptical or fusiform, smooth, hyaline, generally two-celled.

1. Dasyscypha agassizii (B. & C.) Sacc. Syll. Fung. 8: 438. 1889.

Peziza (Humaria) Agassizii B. & C. North American Fungi, no. 713. Grev. 3: 151. 1875.

Gregarious or single, stipitate, 1-2 mm. high and to 4 mm. wide; flattened when moist, concave when dry; hymenium smooth, lemon yellow to orange-yellow; margin undulate, incurved; exterior and short stipe white tomentose, hairs short; spores elliptical to subfusiform, smooth, hyaline, mainly continuous with small guttulae, some show tendency to be uniseptate, 4-7.5 x 2-4 mic.; paraphyses slender, granulate, very slightly clavate, free at tip.

On balsam trunks and dead sticks; St. Louis, July 1886, Holway 179; Cook, Aug. 1903, Freeman & Ballard 70, 141.

This was first thought to be *D. resinaria* and to agree with collections made by A. P. Anderson at Walker, Minn., described in Bull. Torr. Bot. Cl. 29: 1902, but upon farther examination both the spores and ascophore prove to be too large.

Exsiccati: Ellis, North American Fungi. 1311.

2. Dasyscypha borealis (Ell. et Holw.) Sacc. Syll. Fung. 8: 457. 1889.

Peziza borealis Ellis & Holway. Arthur Bull. No. 3: 35. 1887.

Short-stipitate, about 1 mm. in diameter, globose when dry and nearly closed, densely shaggy and fringed with gray hairs, the marginal ones 80-100 mic. long, and 2.5 mic. thick; disk pale; asci cylindrical, sessile, 75-80 by 7-8 mic.; paraphyses stout (2.5 mic. thick), pointed above and slightly exceeding the asci; sporidia clavate-fusoid, nucleate, hyaline, straight or a little curved, 2-seriate, 20-22 x 3-4 mic.

On rotten wood overspread with a brown *Zygodesmus;* St. Louis, July 1896, Holway 264.

The above description is taken from Arthur's Report Bull. No. 3. p. 35. 1887. The herbarium material (Holway 264) does not contain any spores and the external characters harmonize with Sheldon 4194, which is *Lachnella canescens* (Cooke) Phill., as dedetermined by Dr. Durand and the writer, but the spores as described above are too large for *Lachnella canescens* (Cooke) Phill.

4. LACHNELLA FRIES.

Cups gregarious or solitary, fleshy-waxy, minute, sessile, hemispherical, becoming cupulate; exterior villose with yellowish-brown hairs; spores narrowly fusiform, smooth, hyaline, continuous or two-celled.

1. **Lachnella canescens (Cooke) Phill. Man. Brit. Discom. 259. 1887.**
Peziza canescens Cooke, in litt.

Gregarious or scattered, sessile, globose and closed becoming cupulate but never disk-like, when dry nearly globose; scarcely 1 mm. wide or high; hymenium dark brownish; exterior densely villose with yellowish brown hairs, septate, blunt to 3 mic. wide, woolly balls with a dark centre; spores narrowly fusiform some slightly clavate, mainly straight, hyaline, continuous (?), 9-12 x 2-3 mic.; paraphyses filiform, slightly exceeding ascus.

On old naked oak log; Hennepin, April 1891, Sheldon 4194.

The specimens are dried and some, before soaking in water, were nearly white tomentose balls; after being soaked in water, they turned yellow to brown with very dark centres. Some of the hairs appear pale yellow with a colorless tip. *Lachnella corticalis* (Pers.) Fr. is very closely related, differing mainly by growing on bark. (Thümen, Mycoth. univ. 280.) *Lachnea bicolor* (Krieger, Fung. Sax. 1485) also is a close ally but the acute paraphyses are uncommon in the Minnesota specimens and the tendency toward a pseudoseptate condition places the latter under *Lachnella canescens* (Cooke) Phill. Durand has seen some of the specimens and agrees with this determination.

5. SCLEROTINIA FUCKEL.

Cups gregarious, springing from an under-ground sclerotium, fleshy-waxy, stipitate, cupulate or funnel-shaped, large or small; stipe very long, slender, terete, immersed, tomentose near base; exterior glabrous and smooth; spores elliptical, hyaline, smooth, continuous.

1. **Sclerotinia tuberosa (Hedw.) Fckl. Symb. Myc. 331. 1869.** (Plate XIV, Fig. 1. Plate XVII, Fig. 1.)

Octospora tuberosa Hedw. Musci. Frond. 2: 33. t. 10. f. 13, 1788.

One to several cups springing from an irregularly elliptical or subglobose sclerotium buried in the ground; sclerotium externally black, wrinkled, 0.5 mm.-3 cm. in diameter, interior white; cup stipitate, fleshy, thin, first closed subglobose or pear-shaped, expanding to funnel-shaped, finally becoming quite flattened, whole of a bright brown or tan color; margin entire, thin, erect; hymenium even, 1.5 cm. in diameter; exterior and stipe glabrous with stipe tomentose at base, long, tapering downward, flexuous, slender, brown, 3 cm. or more long; spores elliptical, obtuse, smooth, hyaline, 2 small guttulae, 11-15 x 5-6 mic.; paraphyses septate, slightly thickened.

Grows in patches a foot in diameter sometimes, on the ground in moist woods, where *Anemone nemorosa* is very abundant. Sclerotia often are found attached to the roots of *Anemone;* Ramsey, May 1899, 1903, Freeman 303; Hennepin, April & May 1903, Nelson; Hennepin, May 1904, Freeman; Hennepin, May 1906, Hone 799; Hennepin, May 1907, Holway; Hennepin, May 1907, Hone 810, May 1908, Hone 1012, 2005.

Exsiccati: Roumeguère, Fungi Gall. 3337; Sydow, Mycoth. March. 76; Plates: Tulasne, Sel. Fung. Carp. 3. tab. 22. fig. 1-4, Gill. Discom. Franc. pl. 72; Sow. Eng. Fung. 1. pl. 63; Brefeld, Bot. Untersuch. 4. taf. 8; Boudier, Icones Mycol. 3. pl. 477.

6. RUTSTROEMIA KARSTEN.

Cups solitary, small, stipitate, waxy, funnel-shaped; exterior scurvy, dark; stipe long, slender, terete; spores narrowly-fusiform, smooth, hyaline, with many guttulae at maturity stalked.

1. **Rutstroemia firma (Pers.) Karst. Myc. fenn. 1:108. 1871.**

Peziza firma Pers. Syn. Meth. Fung. 658. 1801.

Scattered, stipitate, firm, funnel-shaped; margin incurved, entire; hymenium deep brown when dry, 7 mm. in diameter; exterior and stipe wrinkled, scurvy, lighter brown, stipe often blackish-brown, very long, slender, straight, attenuated downwards, 1-3 cm. long, very variable in length; spores narrowly fusiform, acute, uniseriate, hyaline, continuous, straight or curved, with 2-5 guttulae, 20-24 x 4-6 mic.; paraphyses filiform slender.

Growing on wood (?); Ramsey, Aug. 1893. Sheldon 5618.

A few spores were found with a delicate thread at each end, one

thread bearing a minute and distinct globose head. This character is common in this species and its ally, *R. echinophila,* growing upon chestnut burrs. Sheldon suggested that the specimens might be a *Sclerotinia* but there is no trace of a sclerotium. The preserved specimens appear to have grown upon wood and the field notes do not specify the host.

Exsiccati: Sydow, Mycoth. March. 30 (*Ciboria bolaris*). The spores measure slightly smaller but are of the same character; Plates: Gill. Discom. Franc. pl. 74. fig. 2; Saccardo, Fung. Ital. pl. 1295; Boudier, Icones Mycol. 3. pl. 483.

7. CHLOROSPLENIUM FRIES.

Cups gregarious or solitary, waxy, tough, stipitate, cupulate or irregular, green or olivaceous; exterior glabrous, smooth, often darker than the interior; spores elliptical or fusiform, smooth, greenish, continuous.

1. Chlorosplenium aeruginosum (Oed.) DeNot. Prop. Rett. Disc. 22. 1864.

Elvella aeruginosum Oeder. Flor. Dan. t. 3. Fasc. 9. p. 7. tab. 534. f. 2. 1770.

Gregarious or scattered, turning wood upon which it grows a deep verdigris green, stipitate, tough, glabrous, cupulate, first closed turbinate, finely expanded, very irregular, from cup to ear-shaped or flattened; margin wavy, flexible, even; hymenium often tan to paris-green in color; stipe slender expanding into cup, a deep green, 1 mm. high; spores fusiform-cylindrical, acute, curved or straight, greenish in color or hyaline, smooth, continuous with small guttulae in each end, 10-12 x 2 mic.; paraphyses slender, filiform with tinge of green at the apex.

On rotten wood; Ramsey, 1889, Sheldon 17.

Agrees in every respect, excepting the larger spores, with *Ch. aeruginascens* (Nyl.) Karst. This difference in spore size has been thought by Rehm (178, p. 753), and Lindau (124, p. 196), sufficient basis upon which to distinguish the two species.

Exsiccati: Ellis, North American Fungi. 987; Plates: Grev. Scott. Cryptfl. 5. pl. 241. fig. 1-4; Gill. Discom. Franc. pl. 88. fig. 1; Sow. Eng. Fung. 3. pl. 347.

2. Chlorosplenium aeruginascens (Nyl.) Karst. Myc. fenn. 1: 103. 1871. (Plate XIV. Fig. 2.)

Peziza aeruginascens Nyl. Pez. fenn. 42. 1869.

Peziza aeruginosa (in part of some authors.)

For external characters see *Chlorosplenium aeruginosum* (Oed.) DeNot., from which this cannot be distinguished externally; spores cylindrical or fusiform, acute or obtuse, curved or straight, greenish in color, a small guttula in each end, smooth, continuous, 8 x 1.5-2 mic.; paraphyses slender, tipped with tinge of greenish color. This species turns the wood upon which it grows a deep verdigris green to a considerable depth. Fully developed cups are more rare than the green mycelioid state, as Phillips (162, p. 147) has noted.

Growing upon coniferous wood, birch, and other dead sticks; Cass, Sept. 1898, Freeman & MacMillan 150; Houston, Aug. 1900, Lyon 737; Cook, Aug. 1901, Lyon, Butters & MacMillan; Cook, Aug. 1903, Freeman 4.

Exsiccati: Thümen, Fungi Austr. 831 (*Ch. aeruginosum*, spores measure 8 x 1.5 mic.) Saccardo, Mycoth. Ital. 333 (*Ch. aeruginosum*, spores measure 6-8 x 1-2 mic.); Plates: Tulasne, Sel. Fung. Carp. tab. 20. f. 15-19.

8. CIBORIA FUCKEL.

Cups solitary, small, stipitate, waxy, funnel-shaped to convex; exterior glabrous and smooth; spores elliptical, yellowish, smooth, continuous.

1. Ciboria uliginosa (Fr.) Rehm, Raben. Krypt. Fl. 1: 3: 761. 1896.

Helotium uliginosum Fries, Summ. Veg. Scand. 355. 1849.

Scattered or gregarious, stipitate; cup concave to convex, light-yellow, to 5 mm. across, pruinose beneath; stipe light yellow, to 4 mm. high; spores elliptical, obtuse, smooth, hyaline, with 2 large guttulae, 8-10 x 2-4 mic.; paraphyses very slender, not clavate, branched, up to 2 mic. wide.

On decayed twigs and wood in swamp; Goodhue, Aug. 1893, Anderson 799; Becker, Aug. 1901, Butters 162.

Lindau follows Rehm in considering this a *Ciboria* instead of a *Helotium* or *Hymenoscypha*.

2. Ciboria tabacina Ellis & Holway, Arthur, Bull. No. 3: 35. 1887.

Stem slender, almost filiform, slightly enlarged above, 0.5-1.5 cm. long, and like the outside of the perithecium, yellowish tobacco-brown; cups cupulate-patelliform, 1.5-2.5 mm. in diameter, subrugose beneath, margin entire and even, only slightly incurved; disk slate-colored, concave; asci cylindrical, 100-115 x 9-11 mm.; paraphyses stout, yellowish, gradually but only slightly thickened above;

sporidia uniseriate, elliptical, mostly with a single large nucleus, yellowish-hyaline, 9-12 x 4-5 mic., acute.

On decaying petioles; St. Louis, July 1886, Holway 68.

The above description is taken from Arthur's Report of Bot. Work in Minn. Bull. No. 3. p. 35. 1887.

9. PITYA FUCKEL.

Cups gregarious, minute, fleshy-waxy, hemispherical becoming convex, bright yellow, sessile; exterior white, glabrous, base villose; spores globose, hyaline, smooth, continuous.

1. Pitya cupressi (Batsch.) Rehm, Rabh. Kryptfl. 1: 3: 926. 1896.

Peziza cupressi Batsch. Elench. Fung. 119. 1783.

Gregarious, sessile, or narrowed into a short, stem-like base, pear-shaped and closed, becoming expanded, flattened, fleshy; margin entire, glabrous, thick; hymenium orange-yellow, even, to 4 mm. in diameter; exterior white with short stipe and base downy or villose; spores globose, hyaline, smooth, with one large central gutta, 8-10 mic.; paraphyses filiform.

Abundant on *Thuja occidentalis;* St. Louis, July 1886, Holway 225; Cook, Aug. 1903, Freeman & Ballard 116. 117.

Exsiccati: Thümen, Myc. univ. 718; Ellis & Everhart, North American Fungi. 2322; Plates: Nees, Sys. Schwamme pl. 38. f. 287.

10. HYMENOSCYPHA FRIES.

Cups gregarious or solitary, minute or small, stipitate, concave, tough to firm, waxy; exterior glabrous, smooth; stipe tapering downward; spores elliptical, smooth, hyaline, continuous.

1. Hymenoscypha aspegrenii (Fries) Phill. Man. Brit. Discom. 124. 1887.

Peziza aspegrenii Fries, Sys. Myc. 2: 131. 1823.

Gregarious, stipitate; hymenium deep yellow, exterior lighter to white, glabrous, to 3 mm. wide; stipe white to light yellow when dried, glabrous to minutely pubescent, slender, tapering down, 6-7 mm. long; spores fusiform to elliptical, acute, smooth, hyaline, continuous, biguttulate, 6-9 x 2-3 mic.; paraphyses lanceolate, slender, acute, just the apex longer than ascus.

On sticks and wood on the ground; Hennepin, Sept. 1893, Sheldon 5756; St. Louis, July 1886, Holway 228.

Holway 228 has been determined by Ellis, as *Helotium citrinum* var. *longipes*. As no description or record can be found of such a

variety and since *H. aspegrenii* (Fries) Phill. agrees perfectly with the specimens considered, it is placed there.

Plates: Gill. Discom. Franc. pl. 77. fig. 1.

2. **Hymenoscypha cyathoidea (Bull.) Phill. Man. Brit. Discom. 140. 1887.**

Peziza cyathoidea Bull. Hist. Champ. Fr. 250. t. 416. f. 3. 1791.

Scattered or gregarious, stipitate, cyathiform deeply concave, tough, persistent; margin entire, whitish to tan-colored when old, 1-1.5 mm. in diameter; stipe attenuated downward, glabrous, whitish to tan-colored, to 2 mm. long; spores narrowly elliptical-fusiform, acute, straight or curved slightly, hyaline, smooth, continuous, often with two small guttulae, one in each end, 6-9 x 1.5 mic.; paraphyses scarce, slender, filiform.

On dead herbaceous stems of several herbaceous plants; Hennepin, July 1903, Freeman 1406.

H. cyathoidea (Bull.) Phill. is separated from *Helotium scutula* Pers. by its smaller as well as continuous spores.

Exsiccati: Krieger, Fungi Sax. 1444; Sydow, Mycoth. March. 4170. 1577. 1473. 372; Plates: Saccardo, Fungi Ital. pl. 1324.

11. CYATHICULA DENOTARIS.

Cups solitary, small, firm, waxy, stipitate, concave, margin furnished with acute, ridged teeth; exterior glabrous and smooth; spores fusiform, smooth, hyaline, continuous.

1. **Cyathicula coronata (Bull.) DeNotaris, Pro. Rett. Discom. 381. 1864.**

Peziza coronata Bull. Hist. Champ. Franc. 251. t. 416. f. 4. 1791.

Scattered, stipitate, first closed to subglobose then cup-shaped, glabrous excepting margin, yellowish to tan-colored all over, to 4 mm. in diameter; hymenium even; margin toothed, fringed with acute, whitish teeth, which curve in when young and when dry; stipe slender, 1-7 mm. long; spores fusiform, acute, smooth, curved or straight, continuous, 14-16 x 3-4 mic., with two or more guttulae; paraphyses slender.

On herbaceous stems, possibly nettles lying on moist ground, close to stagnant water in pot-holes of State Park; Chisago, Sept. 1904, Hone 470.

Exsiccati: Sydow, Mycoth. March. 4367; Krieger, Fungi Sax. 1482; Plates: Rehm, Raben. Krypt. Fl. 1: 3: 705. f. 1-5; Lindau, Eng. & Prantl. Nat. Pflanz. 1: 2: 205. f. 160; Saccardo, Fungi Ital.

pl. 1324; Gill. Discom. Franc. pl. 77. f. 2; Phill. Man. Brit. Discom. pl. 5. fig. 26.

12. HELOTIUM PERSOON.

Cups gregarious or solitary, sessile or stipitate, waxy, often thick, plane to repand; exterior glabrous, smooth or pruinose; spores elliptical to fusiform, smooth, hyaline, 2-4 septate.

1. **Helotium citrinum (Hedw.) Fries, Summ. Veg. Scand. 355. 1849.** (Plate XIV. Fig. 6.).

Octospora citrinum Hedw. Musci. Frond. 2, tab. 8, c. 1787.

Crowded into irregular patches, shortly stipitate or sessile, closed, becoming open and quite plane; margin entire, firm; hymenium even, lemon-yellow all over, 1-3 mm. across; spores elliptical, obtuse, smooth, hyaline, with two or more guttulae, continuous, 8-12 x 3-4 mic.; paraphyses filiform, not clavate, slender, branched. Very closely related to *H. confluens* Schweinitz.

On decaying and naked wood; Cass, Sept. 1898, Freeman & MacMillan 166; Hennepin, Sept. 1898, Freeman 241; Hennepin, Oct. 1900, Freeman 922.5; Cook, Aug. 1903, Freeman & Ballard 90; Washington, Oct. 1907, Hone 941.

Exsiccati: Sydow, Mycoth. March. 3475; Jaczewski, Komorov., Tranzschel. 45; Romell, Fungi Scand. 92; Plates: Sow. Eng. Fung. 2. pl. 151; Saccardo, Fungi Ital. 1346.

2. **Helotium herbarum (Pers.) Fries, Summ. Veg. Scand. 356. 1849.**

Peziza herbarum Pers. Disp. Meth. Fung. 72. 1797.

Gregarious, sessile, repand, glabrous, white to yellowish, to 2 mm. in diameter; spores narrowly elliptical, rather blunt, smooth, hyaline, slightly curved or straight, continuous, first with several guttulae, ultimately 1-4 septate, biseriate, irregular, 12-14 x 2-3 mic.; paraphyses filiform, colorless, slender, slightly thickened at apex.

Growing on herbaceous stems; Hennepin, Sept. 1893, Sheldon 5762.

Exsiccati: Krieger, Fungi Sax. 190; Sydow, Mycoth. March. 369, 4365; Ellis, North American Fungi 670; Plates: Gill. Discom. Franc. pl. 89. fig. 2; Saccardo, Fungi Ital. pl. 1363.

3. **Helotium concolor (Phill.) Mass. Brit. Fung-Flor. 4: 247. 1895.**

Peziza concolor Phill. Grev. 8: 102. 1879.

Phialea concolor Sacc. Syll. Fung. 8: 258. 1889.

Gregarious, minute, stipitate, thin, fleshy to tough, pallid or dirty white; exterior finely pubescent; margin minutely fimbriate, 0.25-1

mm. across; stipe to 1 mm. long; spores subfusiform to oblong, hyaline, smooth, tending to become 2 or 4 septate, 6-8 x 1.5-2 mic.; paraphyses filiform, slender.

On rotten log; Wright, May 1900, Freeman 641.

4. Helotium nudum (Phill.) Mass. Brit. Fung-Flor. 4: 498. 1895.

Peziza nuda Phill. Scott. Nat. 6: 124. 1871-1880.

Helotium phillipsii Sacc. Syll. Fung. 8: 220. 1889.

Gregarious, stipitate; hymenium pale-buttery yellow with white rim, first convex becoming plane, to 4 mm. in diameter; exterior and stipe white, glabrous to minutely pubescent; stipe slender, tapering, 6-7 mm. long; spores fusiform, acute, smooth, hyaline, with 2-4 guttulae, finally 1-3 septate, 6-9 x 2-3 mic.; paraphyses long-pointed, longer than ascus, granulated, slender.

On old wood and bark on ground in swamp; Washington, June 1904, Lyon 848.

Massee gives the size as 1 mm. broad by 2 lines high (134, p. 498) while the Minnesota specimens are about double that size; otherwise they agree.

5. Helotium virgultorum var. fructigenum (Bull.) Rehm, Flora p: 160. 1869.

Peziza fructigena Bull. Hist. Champ. Franc. 236. 1791-1798.

Gregarious, stipitate, subglobose to convex or plane, tough; margin entire; hymenium yellow to rufous, 2 mm. in diameter; exterior of cup same color, glabrous; stipe 4 mm. long, 0.5 mm. thick, cylindrical, pale; spores elliptical, slender, acute, curved, tendency towards septa, hyaline, smooth, 14 x 3 mic. seem immature; paraphyses filiform, colorless.

On decaying acorns; Hennepin, Sept. 1889, MacMillan 160; Washington, Sept. 1907, Hone 838.

Exsiccati: Rabh. Fungi Europ. 121; Krieger, Fungi Sax. 189; Thümen, Fungi Austr. 929. Sydow, Mycoth. March. 74; Plates: Sow. Eng. Fung. 1. pl. 117; Gill. Discom. Franc. pl. 73. fig. 3.

6. Helotium scutula (Pers.) Karst. Myc. Fenn. 1: 110. 1871.

Peziza scutula Pers. Myc. Europ. 1: 284. 1822.

Gregarious or crowded, stipitate, cupulate to nearly plane, firm, to 2 mm. in diameter; hymenium ochraceous; stipe slender, white, to 3 mm. long; spores spindle-like, acute, hyaline, smooth, with 2-4 guttulae, ultimately septate, 10-20 x 2-3 mic.; paraphyses filiform, slender, hyaline.

On dead and fallen herbaceous stems, as *Helianthus, Rudbeckia,*

and others, in moist places; Goodhue, Aug. 1893, Anderson 805; Ramsey, Sept. 1896, Freeman 230; Houston, Aug. 1900, Lyon 745; Ramsey, Sept. 1903, Freeman 1384.

The spores of all collections, excepting Freeman 1384, are rather small and do not show septa. They seem to be immature forms of *H. scutula* (Pers.) Karst.

Exsiccati: Sydow, Mycoth. March. 158; Krieger, Fungi Sax. 187 a-c. Plates: Saccardo, Fungi Ital. pl. 1339.

13. CORYNE TULASNE.

Cups gregarious or single, gelatinous, substipitate, concave to plane, minute; exterior glabrous and smooth; spores narrowly elliptical, smooth hyaline, at maturity several-celled.

1. **Coryne versiformis (Pers.) Rehm, Rabh. Kryptfl. 1: 3: 492. 1896.**

Peziza versiformis Pers. Icon. et Descr. Fung. Fasc. 1. p. 25. t. 7. f. 7. 1798.

Scattered, shortly stipitate, tough, cupulate, irregular, glabrous, 1-2 cm. across; hymenium dingy-green to yellowish-green when dried, even; exterior when dry a yellowish-brown with greenish cast; spores elliptical, narrow, straight or curved, hyaline, blunt, smooth, all that were found were continuous, 10-12 x 2-4 mic.; paraphyses slender.

On old rotten stumps; St. Louis, July 1886, Holway 267.

Coryne versiformis (Pers.) Rehm is distinguished from *Chlorosplenium* by its decided yellowish color with none of the clear green cast of a *Chlorosplenium;* also by its lack of power to turn the wood upon which it grows green. The whole subgelatinous consistency of the cup is that of a *Coryne* and not that of a *Chlorosplenium.*

Exsiccati: Ellis, North American Fungi. 988.

Family III. Mollisiaceae.

Mycelium partially or wholly superficial or within the substratum; saprophytic or parasitic; cups superficial or immersed in epidermis at first, fleshy-waxy or cartilaginous or subgelatinous, rarely membranous, globose becoming concave, then plane, sessile, exterior glabrous or hairy, hypothecium forming a distinct layer, exciple composed of dark, more or less rounded, thick-walled cells.

I. TAPESIA FUCKEL.

Cups gregarious or solitary, waxy, sessile, concave then plane, minute; exterior glabrous but scaly; spores elliptical-fusiform, smooth, hyaline, continuous; mycelium superficial, more or less tomentose white, yellow or dark brown.

1. **Tapesia fusca (Pers.) Fckl. Symb. Myc. 302. 1869.**

Peziza fusca Pers. Observ. Myc. 1: 29. 1796.

Gregarious or scattered, sessile upon a subiculum of densely spongy, dark brown, interwoven hyphae, 4-5 mic. wide, hyphae sometimes scanty or almost obsolete; cup convex when young becoming plane with raised margin; margin often irregular, papillose with faint resemblance to hairs; hymenium dirty watery-white to yellowish, 1 mm. in diameter; exterior brown, glabrous; spores elliptical-fusiform, hyaline, smooth, simple, generally eguttulate, mainly continuous, some appear pseudoseptate, 6-9 x 2-3 mic.; paraphyses slender, clavate.

On rotten log; Wright, May 1900, Freeman 642.

Specimens may not be fully mature and thus the spores are small for *Tapesia fusca* (Pers.) Fckl.; nevertheless they agree in color, marginal characters, and size.

Exsiccati: Sydow. Mycoth. March. 1584; Krieger, Fungi Sax. 1035; Plates: Grev. Scott. Cryptfl. 4. pl. 192.

2. BELONIELLA SACCARDO.

Cups gregarious, erumpent, minute, sessile, concave; exterior glabrous black; spores spindle-like, smooth, hyaline, 2-celled; mycelium within the substratum.

1. **Beloniella dehnii (Rabenh.) Rehm, Rabh. Kryptfl. 1: 3: 639. 1896.**

Peziza dehnii Rabenh. Bot. Zeit. 12. 1843.

Gregarious, sessile, 0.5-1 mm. in diameter; hymenium brown; margin inrolled, even, distinct; exterior brownish-black, glabrous; spores spindle-like, straight or curved, narrow, acute, 1 small gutta in each end, smooth, hyaline, 1 septate, 12-15 x 2-3 mic.; paraphyses colorless and needle-like.

On stem and leaves of living *Potentilla;* St. Louis, July 1886, Holway 176.

Exsiccati: Ellis, North American Fungi. 2039; Jaczewski, Fungi Ross. 332; Griffiths, West American Fungi. 193; Plates: Seaver, Discom. Eastern Iowa. pl. 23. fig. 1.

3. CALLORIA FRIES.

Cups gregarious or single, minute, obconic to concave, subgelatinous, sessile or subsessile; exterior glabrous and smooth; spores elliptical, smooth, hyaline, 2-celled.

1. Calloria aurea (Ellis) Sacc. Syll. Discom. 8: 640. 1889.

Ombrophila aurea Ellis, Bull. Torr. Cl. 8: 74. 1881.

Gregarious or single, sessile, first obconic and concave, minute, scarcely more than 1 mm. in diameter, orange or golden yellow all over, subgelatinous, glabrous; spores elliptical, obtuse or slightly acute, smooth, biguttulate, uniseriate and ultimately uniseptate, 8-10 x 4 mic.; paraphyses linear but very scarce.

On rubbish in flower pots in the University Greenhouse; Hennepin, March 1908, Hone.

The above specimens were wholly in the concave stage when found and resembled somewhat externally some species of slime mold. The smooth, biguttulate and uniseptate spores characterize the species.

Exsiccati: Ellis, North American Fung. No. 395.

Family IV. Patellariaceae.

Mycelium wholly within the substratum; saprophytic; cups superficial or immersed in epidermis, leathery or horny, globose or oval, dark-colored, sessile, mainly small, hypothecium and exciple well-developed; paraphyses more or less adherent forming an epithecium.

1. KARSCHIA KOERBER.

Cups gregarious, small, sessile, coriaceous, superficial or slightly erumpent; disk round, plane then convex, black, margin entire and even; spores elliptical-fusoid, smooth, brown, 2-celled, constricted at septa.

1. Karschia taveliana Rehm, Rabh. Kryptfl. 1: 3: 1223. 1896.

Sparingly gregarious, sessile, jet black; margin uneven, wavy, erect, slightly convex when moist; hymenium disk-like or saucer-like, about 1 mm. in diameter, leathery; spores oblong-fusoid, narrow, 1 septate, not constricted, brown, smooth, thick-walled, 12-16 x 4-5 mic.; paraphyses filiform, swollen at tip and brown forming epithecium.

On rotten wood; Sheldon 6237.

The spores are too large for *K. lignyota* Sacc.

Exsiccati: Seaver, Coll. of Iowa Fungi. 87 (determined by Rehm).

2. **Karschia melaspiloides Rehm, Rabh. Kryptfl. 1: 3: 347. 1896.**

Solitary or scattered, sessile, leathery, minute, 1 mm. across, spherical, becoming saucer-like to disk-like when dry, jet-black all over; hymenium shining black; margin entire, erect; spores when young elliptical, obtuse, hyaline, continuous, smooth, becoming elliptical-fusoid, brown, 1 septate, smooth, thick-walled when mature, 12-16 x 5-6 mic.; paraphyses filiform, branching or forking at tip with each apex globose, brown, forming an epithecium by clinging together.

On oak (?) bark; Dakota, July 1893, Sheldon 5319.

3. **Karschia lignyota (Fries) Sacc. Syll. Fung. 8: 779. 1889.**

Patellaria lignyota Fries, Syst. Myc. 2: 150. 1822.

Sparingly gregarious or scattered, sessile, hard, black, spherical to disk-like; margin incurved, distinct, to 0.75 mm. in diameter; spores elliptical-fusoid, smooth, brown, 1 septate, slightly constricted, thick-walled, inequilateral, some are biguttulate; 6-12 x 4-5 mic.; paraphyses slender, clavate, brown at apex, forming an epithecium.

On naked decaying wood; Hennepin, Freeman.

The smaller size of the cup and the smaller spores separate this species from *K. taveliana* Rehm.

Exsiccati: Ellis, North American Fungi. 400; Plates: Saccardo, Fungi Ital. pl. 1411.

4. **Karschia nigerrima Sacc. Syll. Fung. 8: 780. 1889.**

Slightly gregarious, sessile, tough, disk-like, expanded, round; margin rolled in, some almost ball-like; hymenium black, barely 1 mm. in diameter, minute; spores elliptical-fusoid, smooth, brown, 1 septate, often constricted at septa, ends somewhat acute, some are biguttulate, 13-18 x 4-6 mic.; paraphyses slender, clavate, curved, brown at apex, forming an epithecium.

On bark of Betula; Lake, June 1893, Sheldon 4490, 4867.

Rehm (178, p. 347) writes of this species that the smaller-spored forms occur on *Betula* and *Corylus,* while the common form with spores 15-20 x 5-6 mic. occur on *Alnus.* The spores of the material are too large for *K. lignyota* Sacc. which it, however, very much resembles.

Exsiccati: Cavara, Fungi Long. 116; Plates: Saccardo; Fungi Ital. pl. 108.

Family V. Cenangiaceae.

Mycelium within the substratum; saprophytic; cups at first more or less immersed, becoming superficial, often enclosed within a membrane, which disappears with age, leathery, waxy or gelatinous, concave or cupulate, dark-colored, sessile, small, hyothecium and exciple well-developed; paraphyses forming a well-developed epithecium.

1. CENANGIUM FRIES.

Cups caespitose or single, erumpent, leathery, sessile, brown, small; exterior scurvy, whitish; spores narrowly elliptical, smooth, hyaline, continuous.

1. **Cenangium furfuraceum (Roth.) DeNot. Prop. Rett. Discom. 30. 1864.**

Peziza furfuracea Roth. Cat. Bot. 2: 257. tab. 9. fig. 3. 1797-1806.

Caespitose or solitary, erumpent, dry and leathery, sessile; margin entire, incurved, irregular; hymenium naked and smooth, brownish to yellowish-brown, to 1.5 cm. in diameter; exterior white, densely covered with white to rust-colored scurf, or mealy, base narrowed and plicate; spores narrowed, elliptical, obtuse, slightly smooth, hyaline, continuous, 6-10 x 2-3 mic.; paraphyses slightly clavate, brown at apex.

On dead limbs of *Acer spicatum;* Lake, June 1893, Sheldon 4750.

Exsiccati: New Foundland Fungi. Waghorne. 116 (Det. by Peck); Ellis, and Everhart, North American Fungi. 3547; Fungi of Cayuga Lake Basin, N. Y. Jackson 112 (Det. by Durand). Plates: Saccardo, Fungi Ital. pl. 1312; Kalkbrenner, Szepsi Jegy. 2. pl. 3.

2. GODRONIA MOUGEOT.

Cups gregarious or mainly solitary, erumpent, tough to leathery-fleshy, substipitate, globose then urn-shaped, margin concentric striate; exterior blackish-brown, scabrous; spores needle-shaped, smooth, hyaline, 5-7 septate.

1. **Godronia urceolus confertus n. var.**

Caespitose or very rarely single, 1-20 in a cluster, tough to fleshy, erumpent, sessile when young, then stipitate, first globose, cupulate or pitcher or urn-shaped with distinct stipe; mouth first closed, opening with a circular orifice; margin concentric striate, naked; hyme-

nium sunken, concave, gray-white; exterior blackish-brown, scabrous to furfuraceous or vertically striate, sometimes, 0.5-1.5 mm. high, 1 mm. wide; spores needle-shaped, acute, lying in ascus in fascicle, slightly bent or straight, hyaline, smooth, 5-7 septate usually, sometimes more, 40-55 x 0.5-1.5 mic.; paraphyses filiform, very slightly enlarged at apex, colorless.

Breaking through the bark of dead sticks generally in clusters, on *Prunus pumila* L. Cook, Aug. 1903, Freeman & Ballard 100.

The Minnesota specimens differ from *G. urceolus* (Alb. & Schw.) Karst. in habitat (growing upon *Prunus*); the chiefly clustered and stipitate habit; and the slightly shorter spores. Karsten gives for *G. urceolus* (113, p. 112) "Apothecia caespitosa aut solitaria," Rehm (178, p. 238) gives "meist einzeln, seltener zu 5-7 zusammengedraengt" for the same. *G. urceoliformis* Karst. (113, p. 213) and *Cenangium urceolatum* Ellis (Grev. 6: 9) seem to each be confined to a special host, the former on *Vaccinium* and the latter on *Clathra,* while *G. urceolus* seems not to be confined to any one host. *Prunus* is a host not previously given for a Godronia. Both *G. urceoliformis* Karst. and *C. urceolatum* Ellis are described as scattered, solitary, and sessile or subsessile. The exsiccati corroborate these descriptions, namely *C. urceolatum* Ellis, North American Fungi. 990; *C. urceolus* Karst., Roumeguère, Fungi Gall. 1460; *G. urceolus,* Sydow, Mycoth. March. 1167.

3. TRYBLIDARIA SACCARDO.

Cups solitary fleshy-coriaceous, sessile, more or less saucer-like; black, small; margin erect, obtuse; spores pyriform, brown, multiseptate, many celled.

1. **Tryblidaria fenestrata (Cke. & Peck) Rehm, Ann. Myc. 2: 525. 1904.**

Patellaria fenestrata Cke. & Peck, Report 28: 68. 1875.

Blitrydium fenestratum Sacc. Syll. Fung. 8: 805. 1889.

Scattered, dull black, small, irregular to circular in outline; margin rounded, erect; hymenium plane or convex; spores pyriform, multiseptate, brown, 26-28 x 10-12 mic.; paraphyses clavate and dark at the apex.

On dead branches of *Populus tremuloides;* St. Louis, July 1886, Holway 118.

4. DERMATEA FRIES.

Cups caespitose or single, erumpent, sessile, coriaceous, black,

hemispheric becoming expanded, concave, exterior scurvy; spores elliptical-fusiform, smooth, brown at maturity, 2-celled.

1. **Dermatea cerasi (Pers.) Fries, Summ. Veg. Scand. 362. no 5. 1849.**

Peziza cerasi Pers. Tent. Disp. Meth. Fung. 35. 1797.

Solitary or in clusters 2-4, erumpent, sessile, first globose becoming expanded, 2-3 mm. in diameter; margin raised, distinct, wavy, entire; hymenium black, even; exterior scurvy to mealy, brownish-black; spores cylindrical-fusiform, obtuse, thick-walled, first hyaline, continuous, finally brown, one septate, smooth, straight or curved, biseriate, 14-18 x 3-5 mic.; paraphyses gradually clavate, yellowish-brown and ends tangled.

On dead sticks of *Prunus pennsylvanica;* St. Louis, July 1886. Holway 157; Cook, Aug. 1903, Freeman & Ballard 101; Hennepin, May 1906, Hone 803.

Exsiccati: Ellis and Everhart, North American Fungi. 2812; Ellis, North American Fungi. 989 (*Cenangium cerasi*); Roumeguère, Fungi selecti. 6511; Saccardo, Myc. Ital. 673. Plates; Saccardo, Fungi Ital. pl. 1309; Tulasne, Sel. Fung. Carp. tab. 19. fig. 13-17.

5. TYMPANIS TODE.

Cups gregarious or solitary, erumpent, minute, subsessile, black, concave or plane, subcoriaceous, tough when moist; spores minute, hyaline, continuous, innumerable in the ascus.

1. **Tympanis prunastri (Fckl.) Rehm, Raben. Krypt. Fl. 1: 3: 266. 1896.**

Cenangium prunastri Fckl. Symb. Myc. 267. 1869.

Caespitose, springing from a common stroma, erumpent, subsessile, fragile, powdery, blackish-brown, first globose, closed, becoming irregularly expanded, cylindrical, 1 mm. high and wide; ascus broadly clavate, to 18 mic. wide at the apex, very narrow at base; spores innumerable, minute, hyaline, continuous; paraphyses slender, only slightly clavate and brown at apex forming an epithecium.

On dead and fallen *Prunus* branches, abundant; Hennepin, May 1906, Hone 805.

The material seems to present only the pycnidia. *Dermatea Prunastri* (Pers.) Fries, seems to be something different although having the same habitat and appearance. Rehm (178, p. 267) calls attention to this difference. The specimens certainly agree better with the genus *Tympanis* than with *Dermatea*.

2. **Tympanis pinastri Tul. Sel. Fung. Carp. 3: 151. t. 19. fig. 10-12. 1865.**

Solitary or gregarious and caespitose, several springing from a common stroma, erumpent, subsessile, leathery and tough when moist, hard and horny when dry, closed at first becoming expanded with a prominent margin, entire, black, shining all over, 1-1.5 mm. high and wide; hymenium, shining black, even; exterior glabrous; ascus cylindrical thick-walled, 9-10 mic. wide; spores innumerable, minute, continuous, hyaline; paraphyses slender, septate, very slightly thickened at brownish-yellow apex, forming epithecium.

On fallen log of *Abies balsamea;* Cook, Aug. 1903, Freeman & Ballard 171.

Exsiccati: New Foundland Fungi. 96 (*Tympanis laricina* (Fckl.) Sacc.). Plates: Tulasne, Sel. Fung. Carp. 3. pl. 19. fig. 10-12.

6. URNULA FRIES.

Cups generally solitary, leathery, tough, large, stipitate, urn-shaped, closed at first opening by a round or irregular opening, when old turning back and somewhat star-like, black; exterior brownish-black, furfuraceous or coarsely scurvy to tomentose with short, black hairs; spores elliptical, smooth, hyaline, continuous.

1. **Urnula craterium (Schw.) Fries, Summ. Veg. Scand. 364. 1849.** (Plate XVI.)

Peziza turbinata Nees, Syst. Pilze. tab. 37. fig. 277. 1816.

Peziza craterium Schwein. Syn. Fung. Carol. 117. tab. 1. fig. 7-11. 1822.

Urnula microcrater Sacc. Syll. Fung. 8: 549. 1889.

Large leathery fungus, 3-7 cm. wide and 8 cm. high, dark brownish-black, caespitose or solitary, usually long-stipitate, thick, tough, urn-shaped, first closed, hollow, opening gradually by an irregular, circular or stellate orifice leaving the margin notched and involute, often splitting into several rays when old, becoming flattened, almost repand, others retain urn-shape until past maturity or decay; hymenium jet-black to brown black, even, smooth, deeply concave; exterior brownish-black to greenish-black, furfuraceous or coarsely scurvy to tomentose with minute black hairs; stipe long to short, thick, plicate and covered with the minute black hairs; some are almost sessile with base plicate to form thick point of attachment; spores elliptical, obtuse, eguttulate, granular, smooth, hyaline, continuous, uniseriate, 25-30 x 10-12 mic.; paraphyses slender, slightly clavate, brown at apex, septate, not forming an epithecium in mature state;

hypothallus is formed of dense black tomentum, or hairs which in some specimens are very apparent on the substratum.

Growing on buried and decaying sticks of various kinds, very abundant in the early spring everywhere; Hennepin, May 1877, Johnson 633 (*P. pullulus* n. sp. not preserved); Hennepin, April-Sept. 1898, Sheldon 4324, 4649, 5819, 5822; 1899, Freeman 307; 1901, Freeman 988; 1899, Butters; 1899, Wheeler; 1903, Nelson; 1906, Hone 797; Ramsey, April-May, 1892, Sheldon 1971; Cass, May 1900, Freeman 575.

Lindau (124, p. 185.) places *Urnula craterium* (Schw.) Fries under *Peziza craterium* Schw. in the subgenus *Geopyxis,* but our specimens do not agree with the characters as given by Lindau for *Geopyxis* as has been so clearly pointed out by Elsie M. Kupfer (119, p. 137-144.): "the texture of the apothecium of *Geopyxis* is described as fleshy, the stem as short and sometimes thin; while in this plant the leathery character of the cup and the length and thickness of the stem are its noticeable features; one of its most characteristic points is the dense black tomentum which serves as a hypothallus." Durand (67, p. 463-495. pl. 1. 2.) describes and figures the structural characters of the apothecium of the *Pezizaceae* as wholly pseudoparenchymatous with no development of excipulum. Miss Kupfer. l. c. figures the same for *Geopyxis carbonaria* but also holds that *U. craterium* has both hypothecium and excipulum which are mainly prosenchymatous, the chief reason for excluding this species from the genus *Geopyxis. Urnula craterium* must be left where Fries first placed it in the family *Cenangiaceae,* although no true epithecium has been observed nor does it possess an erumpent habit.

Exsiccati: Ellis, North American Fungi. 982. Plates: Schwein. Syn. Fung. Carol. tab. 1. fig. 7-11; Seaver, Discom. Eastern Iowa. pl. 25. fig. 2.; Boudier, Bull. Soc. Myc. France. tom. 14. pl. 11. f. 3.

Order Phacidiales.

Family VI. Phacideaceae.

Mycelium within the substratum; saprophytic and parasitic; cups immersed or superficial, membrane covering hymenium until maturity of the spores, ruptures irregularly, more or less coriaceous, black.

1. RHYTISMA FR.

Cups crowded on a thin, broadly effused, black, crust-like stroma; elongated finally gaping and exposing the pale disc; spores elongate, slender, hyaline, continuous, arranged in a parallel fascicle in the ascus. Species commence as parasites on living leaves forming pitch, black patches and bearing conidia during the autumn and winter. The following spring when the leaves are partially decayed the ascophores or cups are born.

1. **Rhytisma salicinum (Pers.) Fries, Vetensk. Akad. Handl. 104. 1819.** (Plate XIX. Fig. 2.)

Xyloma salicinum Pers. Disp. Meth. Fung. 5. tab. 2. f. 4. 1797.

Stroma forming raised, circular or irregular thick, shining-black patches on the upper surface of the leaves; to 1 cm. in diameter; interior white; ascophore roundish or oblong; spores needle-shaped, acute, curved, continuous, hyaline, guttulate, 60-90 x 1.5-3 mic.; paraphyses filiform, slender, apex wavy, hyaline or tinged brown.

On upper surface of various species of *Salix* leaves, very abundant. Winona, Aug. 1888, Holzinger; Hennepin, June 1890, Sheldon 4242; Cass, Aug. 1890, MacMillan 90; Crow Wing, Aug. 1890, MacMillan & Sheldon 73, 22; Brown, July 1891, Sheldon 714, 846; Pope, July 1891, Taylor 856, MacMillan 4; Brown, July 1891, Sheldon 1077; Traverse, Sept. 1893, Sheldon 7248; Lake, Aug. 1903, Freeman & Ballard 185; Cook, Aug. 1903, Freeman & Ballard 59.

Exsiccati: Thümen, Fungi Austr. 186, 185; Thümen, Mycoth. univ. 1664; Sydow, Mycoth. March. 1652, 3055; Krieger, Fungi Sax. 35; Ellis & Everhart, North American Fungi. 190. Plates: Tulasne, Sel. Fung. Carp. 3. tab. 15. fig. 13-22.

2. **Rhytisma acerinum (Pers.) Fries, Vetensk. Akad. Handl. 104. 1819.** (Plate XIX. Fig. 1.)

Xyloma accrinum Pers. Disp. Meth. Fung. 5. 1797.

Stroma forming raised, irregularly circular, black, thick patches on upper surface of the leaves; exciple composed of olive brown cells giving jet black appearance to the exterior, 2 cm. in diameter; ascophores gregarious on stroma, elongate; spores parallel, needle-shaped, obtuse, base acute, hyaline, guttulate, often curved 60-80 x 1.5-3 mic.; paraphyses filiform, curved or wavy, at apex, hyaline.

On upper surface of various species of *Acer* leaves, very abundant, often destroying whole groves of *Acer dasycarpum* Ehrh., Hennepin, Sept. 1898, Freeman; Chisago, Sept. 1891, Sheldon 4248; Hennepin, June 1891, Butters 122; Lincoln, Aug. 1891, Sheldon 1343; Brown, July 1891, Sheldon 1075; Winona, July 1884, Holzinger; Ramsey, Sept. 1908, Hone 1020; Chisago, Oct. 1908. Hone 1028; Washington, Oct. 1908, Hone. 1084.

Exsiccati: Krieger, Fungi Sax. 185; Thümen, Fungi Austr. 513, 260; Thümen, Mycoth. Univ. 183; Sydow, Mycoth. March. 153; Ellis & Everhart, North American Fungi. 1777; Seymour & Earle, Econ. Fungi. 109. Plates: Tulasne, Sel. Fung. Carp. 3. pl. 15. fig. 9-12; DeCandolle, III. Mem. Gen. Xyloma, pl. 3. fig. 9.

3. **Rhytisma andromedae (Pers.) Fries, Vetensk. Akad. Handl. 104. 1819.**

Xyloma andromedae Pers. Syn. Meth. Fung. 104. 1801.

Stroma forming shining black, very irregular patches on upper surface of leaves; exterior black; interior white; ascophores elongate; spores long and narrowly clavate, apex obtuse, lower half tapering, acute, straight or curved, hyaline, continuous, guttulate, 50-60 x 5-7 mic.; paraphyses slender, apex curled, hyaline.

On upper surface of leaves of *Andromeda polifolia;* St. Louis, July 1886, Holway 186.

Exsiccati: Thümen, Mycoth. Univ. 2177; Sydow, Mycoth. March. 255; Ellis & Everhart, North American Fungi. 2332; U. S. Dept. Agri. Div. Veg. Phys. & Path. 99. Plates: DeCandole, III. Mem. Gen. Xyloma. pl. 3. fig. 13.

4. **Rhytisma solidaginis Schwein. Syn. Am. Bor. no. 2034. p. 241. 1834.**

Stroma forming small black, shining, raised, irregular oval patches upon upper surface of the leaves; to nearly 1 cm. in diameter.

On leaves of *Euthamia graminifolia;* Becker, Aug. 1901, Butters 181.

Gerard (90, p. 114) states that what Schweinitz described is an insect gall. The Minnesota specimens are undoubtedly of fungous origin and have all the appearance of a *Rhytisma*, although no ascophores are apparent.

Exsiccati: Ellis & Everhart, North American Fungi. 3044.

5. **Rhytisma punctatum (Pers.) Fries. Vetensk. Akad. Handl. 104. 1819.**

Xyloma punctatum Pers. Syn. Meth. Fung. 1801.

Stroma forming minute spherical or irregular black bodies crowded together on a yellowish patch, on upper surface of the leaf, up to 1 cm. in diameter, each stroma up to 1 mm. in diameter; spores not present.

On upper surface of leaves of *Acer spicatum;* Cook, Aug. 1903, Fm. & B. 177.

Exsiccati: Ellis & Everhart, North Am. Fungi 1776; Jaczewski Fungi Ross. 288. Plates: Tubeuf and Smith, Diseases of Plants. p. 244. fig. 129.

Order Tuberales.

Family VII. Eutuberaceae.

Mycelium and fructification wholly within the substratum, never coming to the surface, globose or oval or irregular.

1. TUBER.

Ascomata (closed cups) spherical or oval, smooth, or minutely areolate, peridium thin cartilaginous; gleba veined then lacunose, but never powdery; asci short, 4 spored, sack-like; spores oval, hyaline, continuous.

1. **Tuber dryophilum Tulasne, Fungi Hypogaei 147. tab. 5. f. 3. tab. 19. f. 8. 1851.**

Tuber borchianum Zobel. in Corda, Icon. fung. 6: 77. 1854.

Tuber borchii Corda, Icon. Fung. 6. tab. 19. f. 137. 1854.

Ascomata globose or elliptical, irregular, 0.5-1.5 cm. in diameter, firm, smooth, light watery gray; peridium thin; gleba fleshy but firm, white; asci nearly globular, sessile, generally 4 spored; spores spherical to broadly oval, distinctly reticulate, 20-30 x 30-45 mic. or about 30 mic. when spherical.

In black moldy soil; Cook, Aug. 1903, Freeman & Ballard 48.

Exsiccati: R. Thaxter, Kiltung Point. Maine, Sept. 1902.

2. **Tuber lyoni Butters. Bot. Gaz. 35: 427-431. 1903.** (Plate XIV. Fig. 5.)

Ascomata globose or irregularly elliptical, 0.5-2 cm. in diameter, having a distinct scar-like groove along one side, smooth, light chestnut-brown, becoming finally very minutely areolate and blackish; peridium not thick, cartilaginous; gleba violaceous brown, fleshy but somewhat granular; septae arising from the peridium numerous, anastomosing, labyrinthiform, dark translucent; venae externae white, conspicuous, opening externally throughout the length of the groove; asci pedicellate, 1-5 mostly 4 spored; spores elliptical, acutely echinulate, 15-31 x 25-48 mic.

(1) Beneath *Tilia americana* in calcareous clay soil covered with leaf-mold, on a steep bank of southern exposure. (2) In leaf-mold on island in Lake Minnetonka. Hennepin, March 1903, Lyon & Butters 205; Hennepin, Sept. 1903, Nelson.

The above description is taken from Prof. Butters' description (2, p. 431). The type specimens are deposited in the Herbarium of the University of Minnesota, in both the dried condition and in 2 per cent formalin. The plant is closely related to *Tuber nitidum* Vittad. and *Tuber rufum* Pico.

Explanation of Plates.

All photographs are natural size.

PLATE XIV.

Figure 1. Sclerotinia tuberosa (Hedw.) Fries. with sclerotium exposed.
Figure 2. Chlorosplenium aeruginascens (Nyl.) Karst.
Figure 3. Lachnea hemisphaerica (Wigg.) Gill.
Figure 4. Macropodium macropus (Pers.) Fckl.
Figure 5. Tuber lyoni Butters.
Figure 6. Helotium citrinum (Hedw.) Fries.

PLATE XV.

Plicaria repanda (Wahlenbg.) Rehm.

PLATE XVI.

Urnula craterium (Schw.) Fries.

PLATE XVII.

Figure 1. Sclerotinia tuberosa (Hedw.) Fries; photographed in the field.
Figure 2. Discina venosa reticulata (Grev.) Rehm.

PLATE XVIII.

Sarcoscypha coccinea (Jacq.) Cooke.

Plate XIX.

Figure 1. Rhytisma acerinum (Pers.) Fries.
Figure 2. Rhytisma salicinum (Pers.) Fries.

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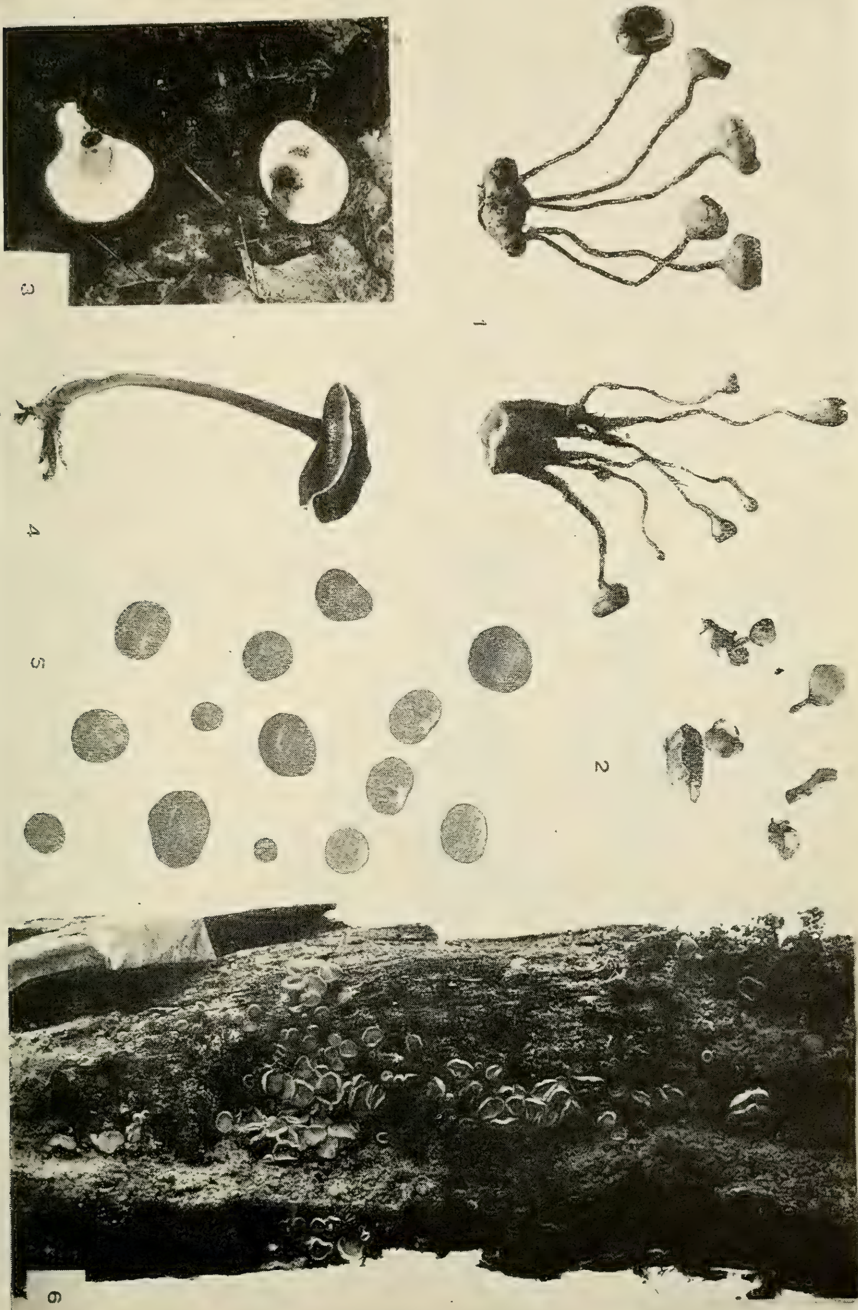

PLATE XIV.

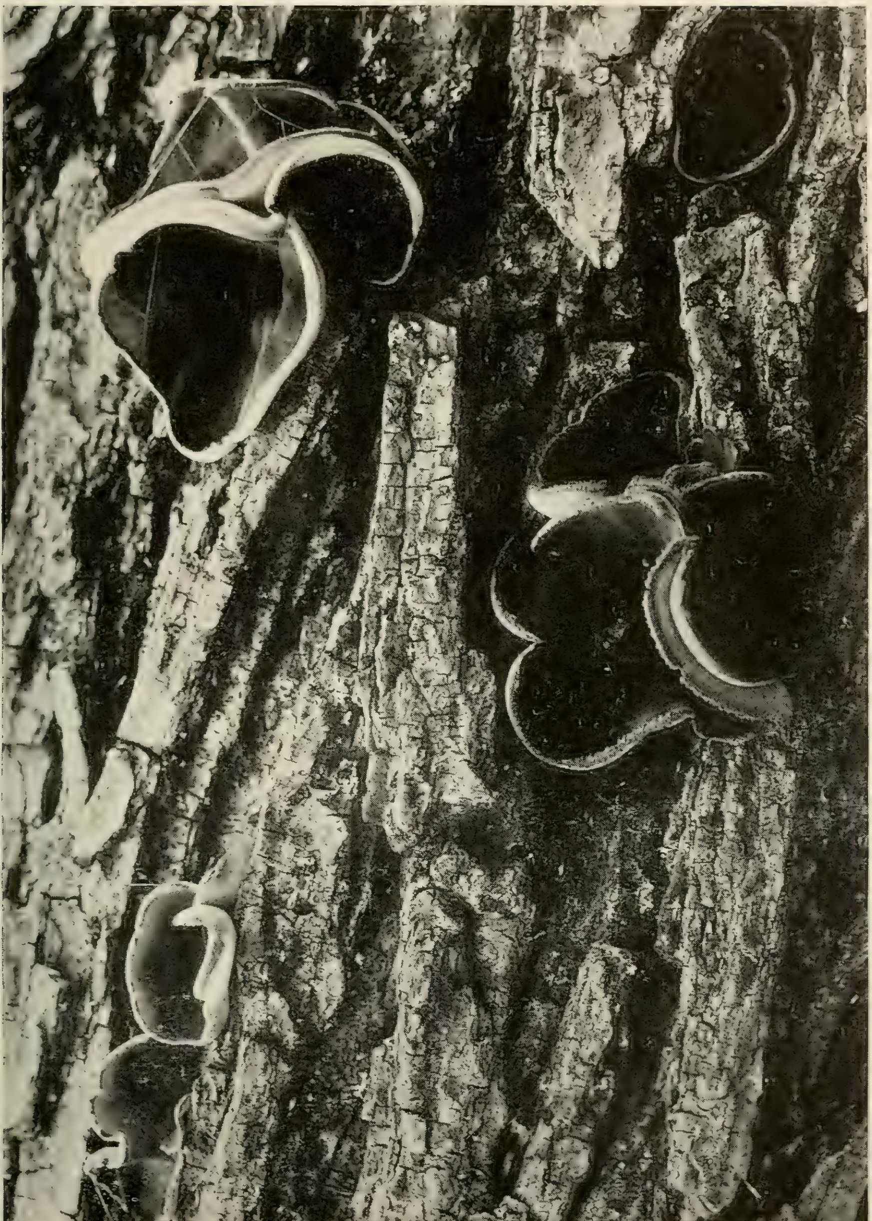

PLATE XV.

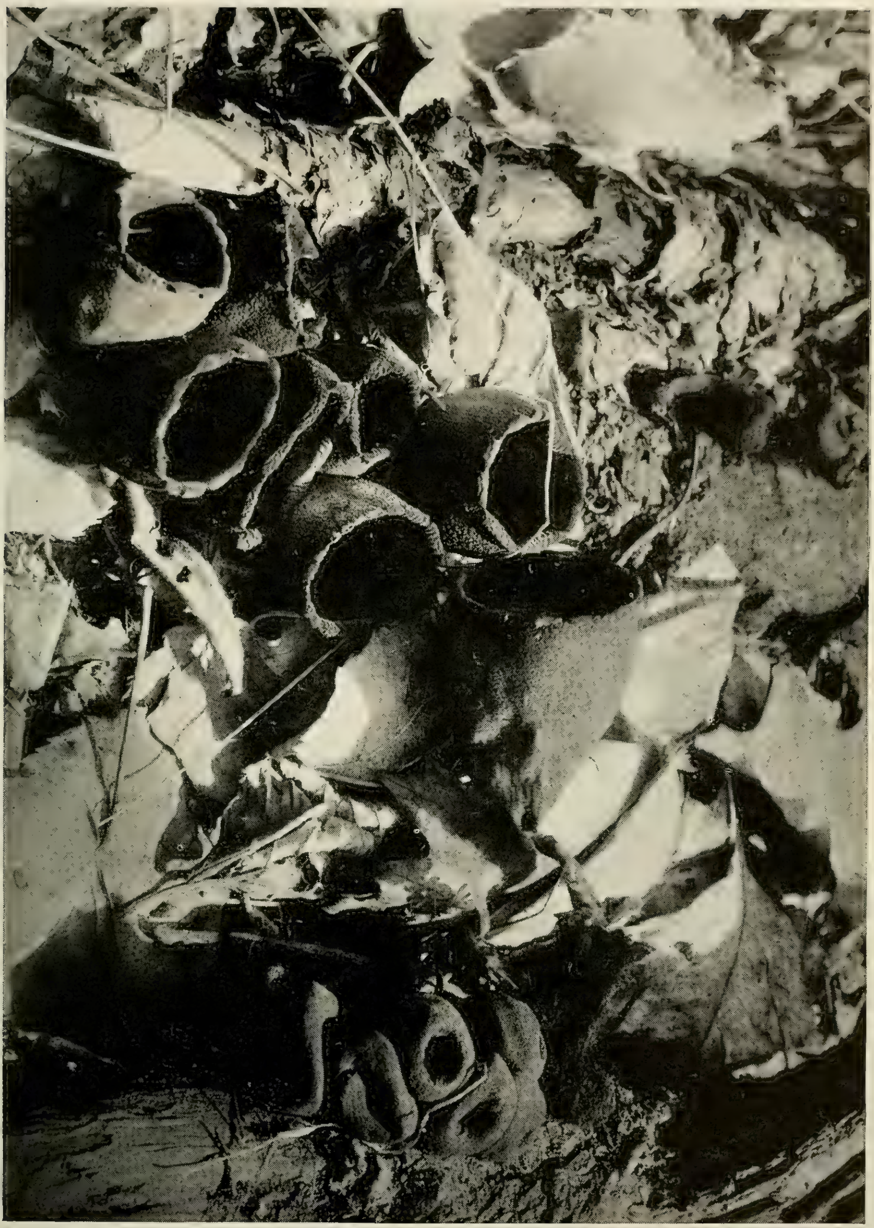

PLATE XVI.

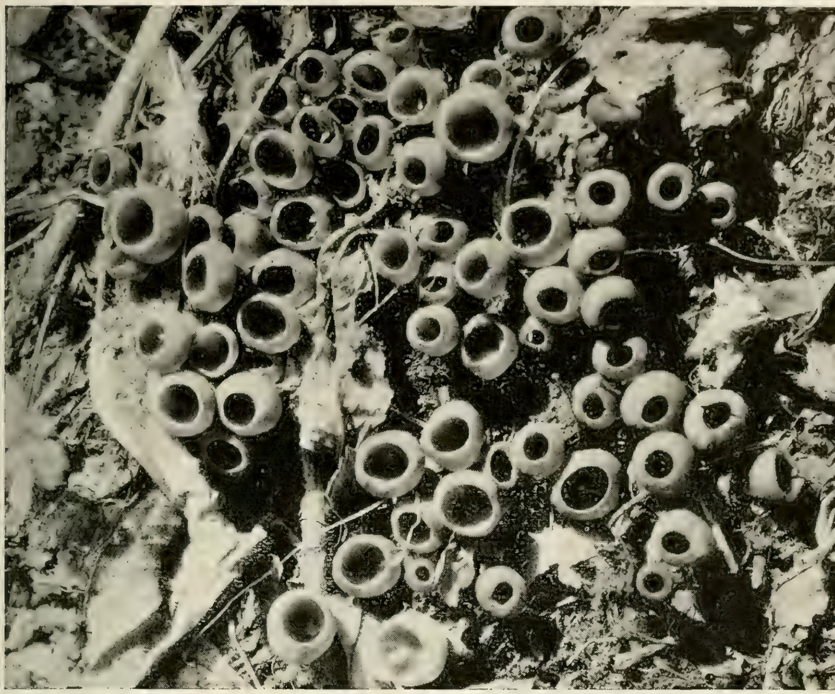

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PLATE XVII.

PLATE XVIII.

PLATE XIX.

6. A NEW GENUS OF BLUEGREEN ALGAE.

FREDERIC E. CLEMENTS
and
H. LEROY SHANTZ.

In studying the algae collected during an ecological investigation of Seven Lakes, a group of alpine lakes just south of Pikes Peak, Dr. Shantz found a form which could not be referred to any known species. The plant was submitted to Dr. Clements, who recognized it as a new genus closely related to *Merismopedia*. This ready recognition arose from the fact that he had frequently stated to his advanced classes that there must be in existence somewhere a form resembling *Sarcina* but bluegreen in color. Material was sent later to Dr. G. T. Moore and to Dr. W. A. Setchell, both of whom stated that in all probability the plant was new. The plant was first collected in a pond on Bald Mountain, the peak just south of Pikes Peak, during August and September, 1903. It was found in the same pond again in August and September, 1904 and 1905. The collection of September 17, 1904 was richest in this form, but the colonies were rare even in this material. The pond is a shallow one, lying at an altitude of nearly 12,000 feet. It is fed by rills from the snowbanks on the mountain slopes which encircle it, and in the short summer by springs. The pond is often frozen over until late in June, and freezes again in October. During the summer of 1904, when the colonies were more frequent than usual, the temperature of the water never exceeded 13 degrees C. Collections were made repeatedly in the neighboring lakes, Seven Lakes, Dead Lake and Lake Moraine, without finding the plant in any of them. This makes it probable that the plant is endemic in the original pond, an assumption borne out by the fact that the pond is in the bottom of a mountain-girt valley, with only an abrupt and narrow outlet downward into the forested subalpine region.

The single cell is identical with that of *Chroococcus*, and the real nature of the plant does not become evidently different until the

8-celled colony is produced (figure 1). Although the growing plant was kept under observation for several months at Lincoln, 1, 2 and 4-celled stages were rarely found, perhaps owing to the rapid division. This probably explains also why the great majority of the cells seen were somewhat oblong, though a sufficient number of spherical cells were found to indicate that this is the normal shape of the cell. The division of the cells is very regular and rapid, and the 8-celled stage is soon followed by the 16-celled colony, and definite groups or families appear in the colony. In figure 2, the 16-celled colony is dividing to form the 32-celled one. The next division produces the 64-celled colony (figure 3), and the succeeding one a 128-celled colony (figure 4 and 5). The latter divides regularly to form the 256-celled stage. The largest colony observed was cubical, and consisted of 512 cells, as shown in figure 6 and 7. The colony shown in figure 6 was observed breaking up into smaller colonies, usually of 8 cells. Some of these smaller colonies broke up into individual cells also. The older colonies often separate into individual cells completely, but more frequently they fragment into smaller colonies, which are one-half or one-fourth of the parent colony. The colonies are always regular in shape and arrangement. Even where a cell has died in a colony, the other cells develop normally. There is no other irregularity aside from unequal growth in different parts of the colony.

Eucapsis nov. gen.

Colonies floating, cubical, regular, when mature consisting of a number of regular families, varying from 8-512 cells, usually of 32-128 cells; cells imbedded in a uniform gelatinous matrix, spherical or elliptical, contents bluegreen, finely granular; cell division in three planes; propagation by fragmentation into separate cells or smaller colonies; Gr. eu-, beautiful, capsis, a small box, referring to the cubical colony.

The genus is related to *Chroococcus* and *Merismopedia,* from both of which it differs in its symmetric cubical colony.

Eucapsis alpina n. sp. Colonies floating, very sparse, 18-80 mic.; cells in a colorless matrix, bluegreen, mostly elliptical from rapid growth, or spherical, 5-7 mic. in diameter, or 6-7 x 10 mic.: the specific name refers to the apparently exclusive alpine habit.

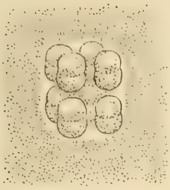
Colorado: In a pond at 12,000 feet on Bald Mountain; collected

by Dr. Shantz in 1903, 1904, 1905. The type specimens are in the herbarium of the University of Minnesota, and in the collection of Dr. Shantz; cotypes are in the collections of Dr. Moore and Dr. Setchell.

Explanation of Plate.

Magnification: 500 in figures 1-7; 3,000 in figure 8.

Figure 1. Late stage of an 8-celled colony.
Figure 2. 16-celled colony dividing to produce a 32-celled colony.
Figure 3. 64-celled colony.
Figure 4. Early stage of 128-celled colony.
Figure 5. Late stage of the same colony.
Figure 6. 512-celled colony.
Figure 7. Surface view of the same colony.
Figure 8. a, normal spherical cell; b, c, d, successive stages of cell division.



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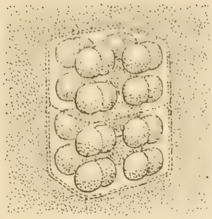

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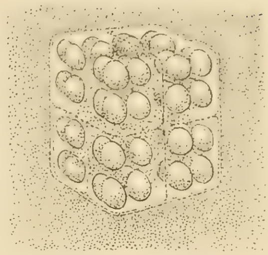

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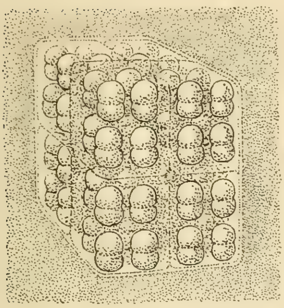

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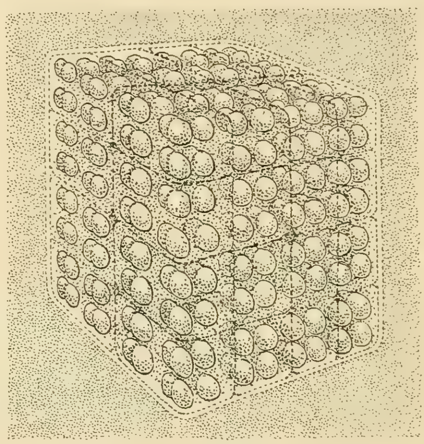

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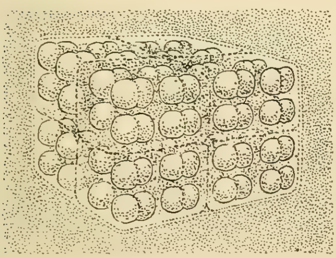

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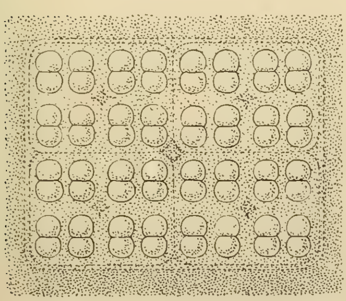

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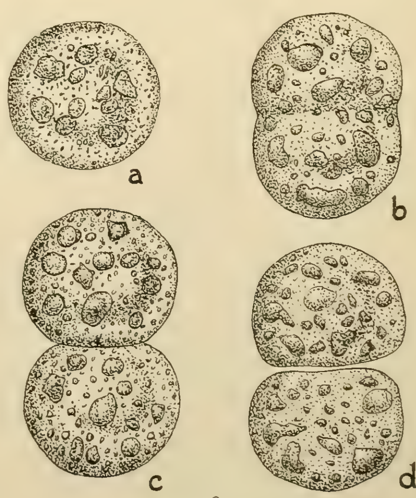

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PLATE XX.

HELIOTYPE CO., BOSTON.

GEOLOGICAL AND NATURAL HISTORY SURVEY OF MINNESOTA
FREDERIC E. CLEMENTS, *State Botanist*

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CONTENTS

OBSERVATIONS ON THE MORPHOLOGY OF THE UNDERGROUND STEMS OF SYMPLOCARPUS AND LYSICHITON, TOGETHER WITH SOME NOTES ON GEOGRAPHICAL DISTRIBUTION AND RELATIONSHIP.

C. OTTO ROSENDAHL.

Some years ago while engaged in the study of the embryology of *Symplocarpus foetidus* the writer noticed that a number of inflorescences found inclosed by the leaf bases at the apex of the rhizome were more or less in a state of decay. Upon removing the foliage leaves one by one it was observed that one or two inflorescences in good condition were succeeded regularly by two to four which were blasted. The peculiar behavior of these well-protected inflorescences led to a more thorough investigation of the structure and the growth of the rhizomes with a view to finding out if possible the cause of the early breaking down of a majority of the flowering shoots.

In the meantime opportunity was also offered to investigate the underground stems of *Lysichiton,* a monotypic aroid genus of western North America, eastern Asia and Japan. This plant bears considerable outward resemblance to *Symplocarpus,* is characterized by a similar mephitic odor, and has about the same habit of growth. In view of the fact that apparently no careful morphological work had been done on fresh material of either species a detailed comparative study was deemed worth while.

The germination of the seeds and the earliest stages in the development of the underground stems have not been observed enough in detail to present a full account thereof at this time. A large number of germinating seeds are now under observation and a brief account will be given later. A number of young seedlings have been seen, all of which show that the rhizomes grow ascending or erect from the outset. Upon germination a varying number of scale leaves (2-3 in *Lysichiton,* apparently a greater number in *Symplocarpus*) appear before any foliage leaves

are unfolded. Their arrangement is spiral from the first, but the divergence is probably not the same as obtains later on.

The mature rhizomes of both species grow vertically or nearly so in the moist mucky soil of their habitat (Plate XXII, Figs. 3, 5) and not creeping as Dr. Krause states.*

The large leaves with wide sheathing petioles are closely crowded at the crown of the stem with inflorescences borne apparently in their axils. At first sight one is therefore inclined to regard these stems as monopodial in structure, but a closer examination reveals their sympodial character. In some of the extra-tropical genera of aroids like *Acorus* and *Calla*, where the rhizomes grow more or less horizontally, there is a tendency for them to elongate and the sympodial nature is more easily recognized. Among these there is also considerable branching. In *Symplocarpus* and *Lysichiton* with upright, deeply buried rhizomes the various joints or axes of the sympodium are greatly reduced in length and branching is almost if not entirely confined to the renewal shoot. In both of these genera growth is extremely slow after the plants have reached the flower bearing age. A large number of plants of *Symplocarpus* have been examined and it has been found that in the latitude of Minneapolis, at least (45° N.), the yearly increase in the length of the stem is only 3-7 mm. Good-sized individuals with rhizomes 20-30 cm. long may range all the way from twenty-five to seventy-five years of age. Perhaps they are even much older, for the rhizomes decay from below as they are gradually pulled down into the soil by the contractile roots (Plate XXII, Fig. 3). *Lysichiton* usually produces more leaves per year than *Symplocarpus* and consequently adds a little more to its stem yearly. On full grown, vigorous plants of both species. from four to seven axes or joints of the sympodium are added each year.

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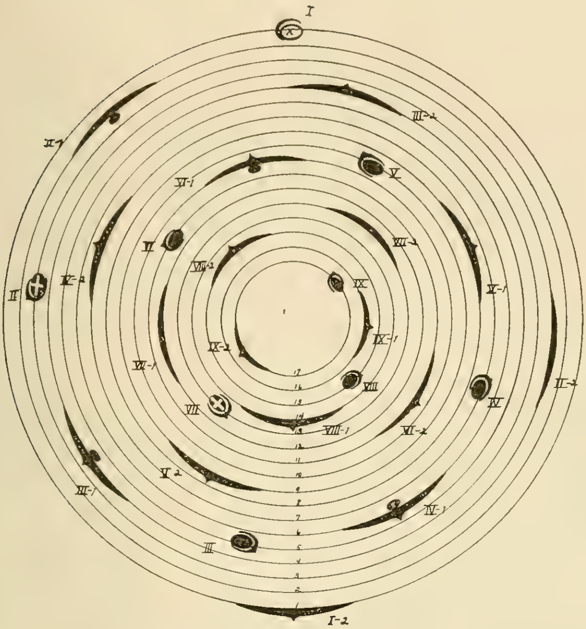
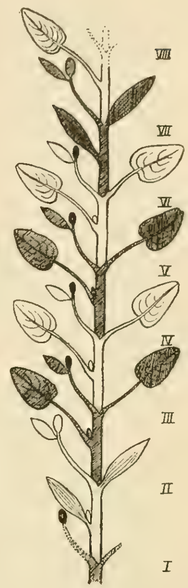
* In a recent monograph on the *Araceae-Calloideae* in Engler's Pflanzenreich, IV. 23B, page 140, Dr. Kurt Krause of the Berlin Botanical Museum makes a series of absolutely erroneous statements concerning the morphology of *Symplocarpus* and *Lysichiton*. It is true that many of the mistakes trace back to Engler's early investigations on these genera, but as long as the monograph appears under Dr. Krause's name one will have to assume that he concurs in everything he copies from his predecessor and that he stands sponsor for the statements, whether borrowed or original, contained therein.

It would seem that when a person undertakes important new monographic work on any group of plants he should investigate his material closely enough to be able to corroborate previous statements of facts, to rectify previous errors, and to add reliable new knowledge to what is already known. Dr. Krause's recent attempt at the *Araceae-Calloideae* fails signally in these respects and can but be harmful to a work of such rank as *Das Pflanzenreich*.



Text Fig. 1. Transverse diagram of the apex of the rhizome of *Symplocarpus* showing leaf arrangement and position of the inflorescences.



Text Fig. 2. Longitudinal diagram of the upper part of the rhizoma of *Symplocarpus* showing scheme of branching. The successive axes of the sympodium are shown alternately shaded and unshaded.

In *Symplocarpus* the plant begins the season's growth by unfolding two scale leaves and one or two inflorescences. These are followed regularly every year by a number of normal foliage leaves, a fact which must appear clear from the accompanying half-tone photographs. Each axis or renewal shoot bears two leaves, a spathe and an inflorescence (Text-Fig. 2). With the exception of the first renewal shoot of the year which bears only scale leaves, all the others, 2-4 in number, unfold ordinary foliage leaves. (Only once has the writer found a third scale leaf, in which case it was the first leaf of the second renewal shoot.) The scheme of branching is shown in a diagramatic manner in Fig. 2.

In Dr. Krause's monograph the scheme of shoot and leaf sequence is given in the following form (Page 141, l.c.):

N, N, Nn, S
N, Nn, S
L, L, L. . . . N, N, S.

In this scheme N and Nn stand for scale leaves, S for spathe and L for foliage leaf. It is quite clear that the scale leaves indicated in the first row are the remains of the sheathing petioles of the foliage leaves of the preceding season. The apex of the rhizomes is situated 10-15 cm. below the surface of the ground and that portion of the petioles which is covered by the soil persists as decaying remnants into the following spring and early summer as is shown in Fig 3, Plate XXII.

Text Fig. 3. Transverse diagram of the apex of the rhizome of *Lysichiton* showing leaf arrangement and position of the inflorescences.

Text Fig. 4. Longitudinal diagram of the upper part of the rhizome of *Lysichiton* showing scheme of branching.

It is perhaps this confusion of remnants of old petioles with true scale leaves that has given rise to the absurdly erroneous statement about *Symplocarpus* contained in the following sentence: "Herba magna rhizomate crasso, altero anno folia, altero cataphylla atque inflorescentiam proferente" (page 150 l.c.).

To make clear this singular behavior of *Symplocarpus,* Dr. Krause has appended an imaginative original drawing showing the plant in its flowerless year.

It is hardly necessary to add that no such seasonal alternation in the production and unfolding of foliage leaves and inflorescences ever occurs in the life history of *Symplocarpus foetidus.* The accompanying photographs ought to dispel all such illusions even among the most imaginative.

Lysichiton camtschatcense does not agree closely (as stated on page 148 l.c.) with the reputed morphology of *Symplocarpus* nor with the one that actually obtains. There are some differences between the two which appear quite fundamental and of much importance in considerations of relationship while others seem to be later acquirements.

The most obvious, although not the most signficant, of these differences is the lack of any sharp differentiation between the leaves of the main rhizome into cataphylls and foliage leaves as in *Symplocarpus.* This probably can be accounted for, at least as far as the North American distribution is concerned, by climatic conditions. The plants of *Lysichiton* which were studied grew on the west coast of Vancouver Island and in the vicinity of Seattle,* regions where the seasons are much less extreme than in Minnesota.

The last two or three leaves produced during the late summer and fall become much reduced in size, but they resemble the ordinary foliage leaves in form and color and do not partake of the nature of scale leaves in the same degree as those in *Symplocarpus.* They never assume a brownish red color and they are always differentiated into petiole and blade. Some of these reduced leaves evidently persist through the winter and when vigorous growth is resumed in early spring the inflorescences and large foliage leaves follow them in regular sequence. (Text-Fig. 4). In this plant from three to seven renewal shoots are produced each year. Each renewal shoot bears two foliage leaves, two narrow, colorless scale leaves that stand on either side of the shoot just where it bends away or comes out from the main rhizome (Text-Fig. 4). They are more or less entirely enclosed by the large sheathing petioles of the foliage leaves even dur-

* Fresh material was obtained from Seattle in 1910 and 1911 through the kindness of Mr. D. J. Lothrop, to whom the author is very much indebted.

ing the stages of flowering. The shoot ends with a rather large cream-colored spathe and an inflorescence. The spathe enwraps the flowering shoot from the base to within a short distance below the flowers, but is not fused with it at all. The two colorless scale leaves that subtend the spathe are long, narrow and triangular in cross section and show no trace of lamina. Since they became enclosed by the leaf petioles, due to the deep placement of the rhizome in the ground their function, whatever it may have been, has been lost and they remain on the plant perhaps for no other reason than that the plant has not been able to get rid of them.

In both genera the internode between the first and second leaf of the renewal shoot is extremely short, and in this respect there is no difference between them. In *Symplocarpus* the internode between the second leaf of the renewal shoot and the spathe is considerably elongated, measuring 15-20 cm., and the spathe is borne close up to the flowers. In *Lysichiton* the internode between the second leaf of the renewal shoot and the lowermost scale leaf, as well as the one between the two scale leaves and the one between the upper scale leaf and the spathe are all very short. In fact the two scale leaves and the spathe appear to come out at the same level (Plate XXII, Fig. 5). The last internode of the renewal shoot is comparatively very long, frequently measuring 3-4 dm.

In each genus vegetative buds are developed in the axil of the lowermost leaf of the renewal shoot, although their occurrence is not as regular in *Lysichiton* as in *Symplocarpus* (Text-Figs. 2 and 4). It is probable that these buds are produced regularly, but that they are arrested earlier in some cases than in others and that on account of their small size they are readily overlooked. In no case so far as has been possible to ascertain do they develop into lateral shoots. The renewal shoot arises always in the axil of the upper foliage leaf.

The two diagrams shown in Text-Figures 1 and 3 respectively illustrate the arrangement of members at the apex of the rhizome. The concentric circles represent in each case the number of leaves that can be distinctly recognized at any one time. From the two diagrams it can readily be perceived that the 5/13 phyllotaxy obtains in both genera. In *Symplocarpus* it is difficult to make out

the leaf arrangement because it is hard to trace anything beyond the 15th or 16th leaf (Text-Fig. 1). In *Lysichiton* it is much easier because 28 to 30 leaves are easily recognizable (Text-Fig. 3), and in addition the bases of old foliage leaves persist longer.

The arrangement of the leaves is very regular and constant and there is no break in the spiral in passing from one joint of the sympodium to another. The scale leaves and the spathe upon the axis above the second foliage leaf follow the same divergence as can be seen at inflorescence V, (Text-Fig. 3), where these leaves are designated by the letters α, β, γ. There is not, however, any consistency as to which way the spiral runs, for in some plants examined it ran to the right, in others to the left. In both these diagrams it will be noticed that the inflorescence of each renewal shoot is situated just opposite to the upper or second leaf of the shoot.

The number of inflorescences produced each year in *Symplocarpus* is equal to half the sum of scale and foliage leaves unfolded during the season. Usually only one of these inflorescences comes above ground and flowers each year, in which case it is the one that terminates the renewal shoot bearing the two scale leaves (Text-Fig. 1). Where, on the other hand, two inflorescences come up the first belongs to the renewal shoot that bore the last two foliage leaves of the previous season (Text-Fig. 1). More often the inflorescence of this shoot decays, in all probability because it falls outside the first scale leaf and is protected only by the bases of decaying foliage leaves of the previous season. In no case have more than two flowering shoots been observed above ground on one plant.

The remaining inflorescences of the year, or in other words those following the first foliage leaf of the season, do not come to maturity. In all the plants examined they usually appeared blackened and showed signs of decay many months before the leaves were to have been unfolded. In both species the inflorescences are laid down and can be recognized as small buds in among the sheathing petioles some 18-20 months previous to the time of blossoming.

In *Lysichiton* the number of inflorescences produced each year is equal to half the number of foliage leaves (counting the reduced leaves also as foliage leaves), so that in this respect its

behavior is similar to *Symplocarpus*. However, as the total number of leaves produced each season is greater in *Lysichiton* than in *Symplocarpus,* the number of inflorescences laid down each year is also larger than in that genus. Whether this is due to the longer growing season which obtains in the region where *Lysichiton* is native or to an ancestral habit cannot be definitely stated. Five to seven renewal shoots, and consequently as many inflorescences, are not uncommon on vigorous plants (Text-Fig. 4). More of these mature each season than in *Symplocarpus*. Most of the plants have two to four and even five flower stalks (Plate XXI, Fig. 2). It is very likely that sometimes all the inflorescences which are laid down mature, especially on plants producing only four or five renewal shoots each year, for not infrequently one finds on such plants remains of last year's flowering stalks among the decaying bases of the last normal foliage leaves of the same season. On the larger plants blasted inflorescences are frequently found among the bases of the foliage leaves. They do not, however, seem to be as reguarly confined to the latter part of the season's growth as in *Symplocarpus*.

The difference in the behavior of these two northern aroids in regard to the maturation of the inflorescences and in the specialization of some of the leaves is perhaps largely to be accounted for, as has already been stated, by the climatic conditions under which they live. In the case of *Symplocarpus* a long cold winter season has to be endured, during which time all life activities completely cease. The spring transition period and time for blossoming is short, so that the summer season and time for active vegetative growth soon follow. The seasons are extreme and the transition between them rapid, and as a result a very pronounced rhythm has been established in the life of the plant. The period favorable for blossoming has become so short that most of the inflorescences made for each year never reach maturity. The modification of several foliage leaves into highly specialized colored scale leaves are adaptations made to reconcile the early blossoming habit with the cold spring that is encountered.

In the case of *Lysichiton* no such seasonal extremes are experienced. The milder winter season passes gradually into a much earlier spring, spring is more prolonged and grades into a moderate summer. The result is that fewer inflorescences be-

come blasted and that the leaves are less modified through ecological adaptations.

The root system of these two aroids is so remarkable that it deserves at least a passing notice in this connection.

The seeds germinate at or near the surface of the ground, but the young rhizomes are soon pulled down into deeper layers of the soil by the contractile roots. In *Symplocarpus* two and three year old seedlings, often with the seed still attached, have their short rhizomes 3-6 cm. deep in the ground.

The roots are produced in very large numbers and cover the rhizomes very thickly as can be seen in Figs. 3 and 5, Plate XXII. The plant to the left in Fig. 3 has 132 roots by actual count and those in Fig. 5 195 and 200 each. At first these roots are smooth and perfectly white in color (Fig. 3). They soon assume a yellowish brown color and begin to show characteristic transverse furrows and ridges which indicate that they are shortening and exerting a downward pull upon the rhizome. The greatest amount of contraction is in the upper part of the roots. Their contractility can easily be demonstrated simply by pulling on them until the furrows disappear. Upon being released they shorten up again like a rubber band and become wrinkled.

The rhizomes are of such large dimensions (2.5-5 cm. in diameter), that even though the plants grow in moist ground and mucky places, they offer great resistance to being forced end downward into the soil. They encounter roots and underground stems of other plants as well as pebbles, rocks, etc., and old rhizomes show the effect of such resistance by the lower end being worn perfectly smooth and having no traces of roots, leaf scars and other inequalities of the surface (Plate XXII, Fig. 5). The plants of *Symplocarpus* illustrated in Fig. 3 are both comparatively young, the rhizomes having only within the last four or five years attained their full diameter, and no wearing off is as yet perceptible at the lower end. When too great an obstruction is met the lower end becomes deflected and the stem will then assume a more or less oblique instead of erect manner of growth.

Relationship: According to Engler's classification *Symplocarpus, Lysichiton* and *Orontium* constitute the tribe *Symplocarpeae* of the sub-family *Calloideae*. Only one more tribe, the *Calleae,* consisting of the single monotypic genus *Calla* is included in the

sub-family. The whole group numbers only four species and is thus, with the exception of the *Pistioideae,* the smallest sub-family in the *Araceae.*

According to the recent monograph quoted from above, the *Calloideae* occupy a place half way between the *Pothoideae* and the *Philodendroideae.* The present writer admits altogether too limited a knowledge of exotic aroids to pass judgment upon the naturalness of such a classification. As to the interrelationships of the various genera within the *Calloideae* it does not seem that Engler's system is consistent.

The one characteristic which is regarded as of great systematic significance, and practically the only one that could justify keeping these genera together in the same sub-family, is the presence of simple or unbranched latex ducts in connection with the phloem of the vascular bundles. In *Calla* and *Orontium* these ducts show up very clearly in fresh material, especially after treatment with potassium bichromate, but they occur in neither *Symplocarpus* nor *Lysichiton.* Both fresh and preserved material of both genera has been repeatedly examined but no trace of them has ever been found. Scattered tannin cells which stain the same way as the latex ducts with potassium bichromate are frequently found in various parts of the cortex in all the genera of the *Calloideae,* but no special significance has ever been accorded to these.

If a great deal of importance is to be attached to the presence or absence of these latex ducts then both *Symplocarpus* and *Lysichiton* must be separated from *Calla* and *Orontium* in the *Calloideae* and brought into some other position in the system. *Symplocarpus* and *Lysichiton* no doubt are more closely related to each other than they are to the other genera of the subfamily. This relationship will be considered more in detail.

The flowers are monoclinous in both genera and are built on the same plan. The perianth and androecium each consist of two dimerous cycles or whorls. In *Lysichiton* the ovary is two-celled with a single ovule in each cell. The ovule grows out exactly in the middle of the septum and is partly bent with the micropyle towards the base of the chamber. In *Symplocarpus* one chamber occurs in the ovary with a single orthotropous ovule pendant from one side of the upper part of the cavity. In both genera

the ovary is sunk in the fleshy axis, but more deeply in *Symplocarpus* than in *Lysichiton.*

In both genera there is a considerable development of tissue from the antipodal cells at the same time that the endosperm is formed. The details of embryology are different in the two.* In *Symplocarpus* a short thick suspensor is developed, whereas in *Lysichiton* no such organ is present. The mature embryo of the former is almost spherical, while in the latter it is oblong, slightly bent and is flattened on one side. In *Lysichiton* there is no endosperm and the seedcoat is thin. In *Symplocarpus* neither endosperm nor seedcoats are present, the embryo when mature lies naked in the cavity of the ovary and is protected by the enlarged spadix and the hardened perianth.

The inflorescences of *Symplocarpus* and *Lysichiton* are quite unlike. In the former it is short, ovoid completely inclosed by the persistent sessile spathe, whilst in the latter it is long, cylindrical and is freely exposed even before anthesis. The long spathe drops off very early.

The anatomy of root, stem and leaf is much the same in both. It does not reveal anything that can be considered of any special significance in considering relationships. The fact that latex ducts are not present in connection with the phloem of the vascular bundles of either genus does not necessarily mean that they are closely related genetically. There are aroids of widely different relationship in which these structures are lacking.

All things considered, it appears that the relationship of these two aroids is rather remote, especially if one rids himself of the notion that they must be closely related simply because one finds them in juxtaposition in some natural system. If they trace back to a common ancestral branch, which is not at all certain, their separation must have taken place at some very distant time, for the differences in the morphology of renewal shoots and inflorescences appear much more fundamental and significant than the curious similarities in growth and habit which largely seem responsible for the close association of the two genera in systematic works. The latter are apparently nothing more than inter-

* Campbell, D. H. Annals of Botany. XIV. p. 1. Rosendahl, C. Otto. Minnesota Botanical Studies. IV. p. 1.

esting parallelisms and as such do not carry much weight.

Of the two genera *Symplocarpus* is the most highly specialized and should be regarded as phylogenetically farther advanced than the other. This is shown among other things in the colored scale leaves developed in place of the normal foliage leaves, in the blasting of a majority of the inflorescences, and in the complete destruction of the seed coats by the embryo.

In *Lysichiton* some of the foliage leaves only become reduced in size but do not take on a different color. Two ancient scale leaves are still retained on the renewal shoot although they are so inclosed as to be non-functional. Most of the inflorescences laid down come to maturity and the embryo does not destroy the seedcoats.

Geographical distribution: The two monotypic genera have a somewhat peculiar yet not unusual geographic distribution. *Symplocarpus* is found in wet, springy places of eastern North America from Nova Scotia to North Carolina and ranges westward as far as Minnesota and Iowa. Its northern limit seems to be southern Quebec, Ontario and Lake Superior. It is also recorded from eastern Asia in the Amur region and from Japan.

Lysichiton occurs in swamps and boggy places of the forests of the Pacific coast from Alaska to northern California and ranges eastward in Canada as far as the Beaver River Valley and the Columbia River in the Selkirk mountains. It has been reported from Isle Royale in Lake Superior, but the report has not been substantiated by any authentic collection. It occurs in Japan, on the island of Sakhalin and in Kamschatka, from which place it was originally described by Linnaeus.

Such a wide geographical distribution is remarkable when the fruits and seeds are taken into account. No special devices for dissemination have been developed. The fruits are dry and inedible, the seeds large and heavy. In *Symplocarpus* the almost spherical embryos are larger than good-sized peas, in *Lysichiton* the seeds are about half that size. They both contain a large amount of stored food in the form of starch, and in the case of *Lysichiton* at least, are eagerly sought by squirrels. These animals sometimes devour the seeds directly from the plants, at other times they climb upon convenient stumps and branches where they sit and shell out the seeds and now and then drop some of them

to the ground. Sometimes partly devoured fruits are left and in these ways the seeds become scattered.

Whether *Symplocarpus* is disseminated in the same manner or not the writer is not prepared to say. It is very likely, however, that both genera have their seeds distributed chiefly by rodents, such as squirrels and chipmunks, which in carrying the fruits off to desirable places to eat them, drop an occasional seed, or else store them away for future use and forget the hiding place.

It would seem that plants relying on such uncertain methods of seed distribution must be extremely slow migrants and that therefore it has taken these two aroids an enormous length of time to come to occupy so wide a geographical area as they do at the present day.

The present geographical distribution of the two genera points to an Asiatic origin and since the *Araceae* are essentially a tropical family they must have originated somewhere in the eastern tropics. From thence their course of migration was northeastward into Japan, Kamtschatka, the Behring Straits region and across to the American continent. Upon reaching America they wandered south and east into their present areas. It is not likely that they migrated simultaneously to America but rather that *Symplocarpus* had a much earlier advent and gained a great eastward extension at a time when conditions for east and west migrations were better than they became at subsequent periods. *Lysichiton* appears to be a later immigrant and probably found the present geographical and climatic barriers to limit its range.

Summary and Conclusion.

1. Upon germination the seeds of *Symplocarpus* and *Lysichiton* produce 2-several scale leaves before foliage leaves appear. The leaf arrangement is spiral and the rhizomes grow erect from the outset.

2. The rhizomes are sympodial in structure and are made up of a very large number of renewal-shoots. They grow vertically in the soil.

3. Growth is extremely slow so that only 3-7 mm. are added each year to the top of the rhizomes. Large specimens

20-30 cm. in length are estimated to range from 25-75 years in age.

4. In *Symplocarpus* the season's growth begins with the unfolding of two scale leaves. A variable number of renewal shoots are added each year. Each renewal shoot bears two leaves (either scale or foliage leaves), a spathe and an inflorescence.

5. In *Lysichiton* the season's growth begins with the unfolding of ordinary foliage leaves. Three to seven renewal shoots are added each year. Each shoot bears two foliage leaves, two long narrow colorless scale leaves, a long petioled spathe and an inflorescence.

6. In *Symplocarpus* the first two internodes of the renewal shoot are extremely short, the third is considerably elongated, 12-16 cm., while the last, the one between spathe and inflorescence is short. In *Lysichiton* not only the first two, but the three following ones are very short. The last internode of the shoot is greatly elongated, measuring from 3-4 dm.

7. Vegetative buds are regularly laid down in the axil of the second foliage leaf of each renewal shoot. but they are never known to develop.

8. The leaves are all arranged according to the 5/13 phyllotaxy. The spiral may run either clockwise or counter clockwise.

9. The number of inflorescences laid down each year is the same as the number of renewal shoots (3-7), but of this number only one or two in *Symplocarpus* and two to four in *Lysichiton* come to maturity. The remaining ones are blasted many months before the time when they would blossom.

10. The inflorescences can be distinguished 18-20 months before they are to blossom out.

11. A very elaborate system of thick contractile roots is built up in each species. As many as 100-200 roots are found on ordinary sized rhizomes at one time. These roots pull the thick rhizomes end first into the ground.

12. The relationship of the *Calloideae* is not a natural one and *Symplocarpus* and *Lysichiton* should be separated from the group on both morphological and anatomical grounds. The two genera are not very closely related although they show interesting similarities in growth and habit.

13. The present geographical distribution of *Symplocarpus*

and *Lysichiton* point to an east Asiatic origin of both genera. The much greater eastward extension in North America of *Symplocarpus* indicates a much earlier advent of this genus in North America than *Lysichiton*.

14. In all probability *Symplocarpus* and *Lysichiton* trace back to tropical ancestors with above ground stems. Living in a warm and perhaps moist climate they grew and blossomed throughout the year with very little interruption or cessation of growth. They added a number of renewal shoots, perhaps 6-8, and had time and material enough to complete the growth of each one. Each renewal shoot bore two large foliage leaves on its main thickened portion, and upon the thinner more elongated part from one to three bracteal leaves, one of which was the spathe. The foliage leaves were all alike and separated by more or less distinct internodes. If the stems were erect growing the leaf arrangement was probably spiral, but the divergence may have been greater than 5/13.

As the ancestors of these genera, perhaps almost identical with the present ones in floral structure, migrated slowly northward they gradually underwent changes. First came the shortening of the axis and the closer crowding of the leaves. As colder climates were encountered it was found necessary to bury the stem underground in order to live through the unfavorable season. If the stems had been in the habit of branching this was given up as they became very thick upright rhizomes. The foliage leaves became very closely set, a few of them were reduced in size, and in the one case they became modified into true scale leaves.

The habit, however, of producing a number of renewal shoots each year and terminating each one of them with an inflorescence and the associated bracteal leaves was so strongly established in the life history of the plants that it still persists, in spite of the fact that under the rigors of a climate to which the plant was not born, the largest number of these inflorescences are made entirely useless and perish early.

EXPLANATION OF PLATES.

PLATE XXI.

Fig. 1.—A group of *Symplocarpus* plants shortly after blossoming. A number of foliage leaves are fully expanded, others are being unfolded. The middle specimen also shows the two scale leaves at the base.

Fig. 2.—A single plant of *Lysichiton* with 8 or 9 foliage leaves and 3 fruit stalks.

PLATE XXII.

Fig. 3.—Two young plants of *Symplocarpus*. A number of roots have been cut away to show the rhizome and the upright manner of growth is evident. The remnants of old petioles are shown just above the roots. The specimen to the left shows two scale leaves on the outside. The spathe and the sharp cone of rolled up foliage leaves are just breaking out. The specimen to the right shows two flowering shoots; one outside the scale leaves, the other enclosed by them.

Fig. 4.—The apex of the rhizome of *Lysichiton* with many of the foliage leaves cut away. The two narrow scale leaves with a blasted inflorescence between them are shown photographed in place.

Fig. 5.—Two specimens of *Lysichiton* after having been packed and transported from the west coast. The leaves as a consequence are more or less frayed and distorted. The specimen to the right shows how the older parts of the rhizome are worn smooth by contact with the soil. The two long, narrow and colorless scale leaves are clearly seen and the spathe is still attached to the flowering shoot. A number of old petioles were removed to expose the base of the shoot.

Fig. 1

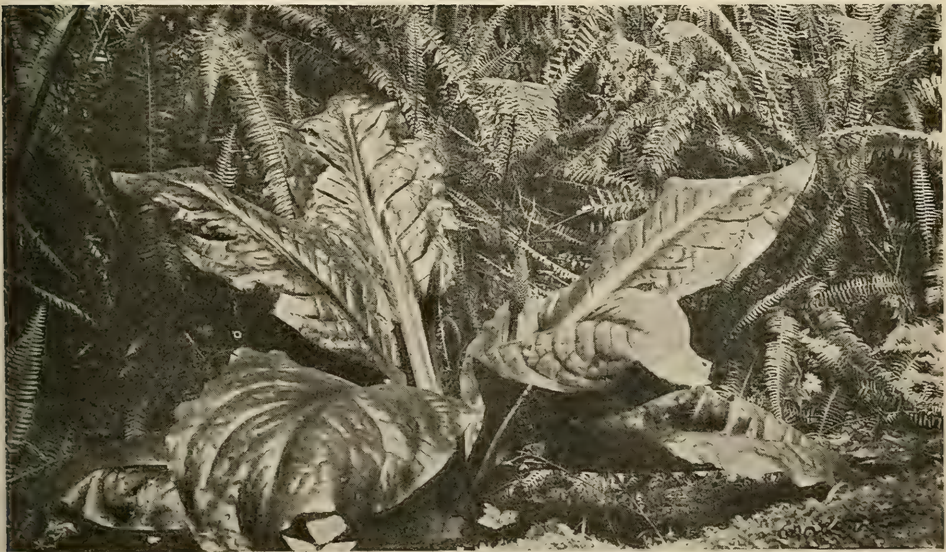


Fig 2

PLATE XXI

Fig. 3

Fig. 4

Fig. 5

PLATE XXII

SOME EFFECTS OF SEVERE FROST UPON VEGETATION IN A CONDITION OF ACTIVE GROWTH.

FREDERIC K. BUTTERS AND C. OTTO ROSENDAHL.

INTRODUCTION.

The spring of 1910 was exceedingly early in Minnesota. Following a winter with heavy early snowfall and almost no frost in the ground March was 6 degrees (C) warmer than usual—about the temperature of a normal April. There were a few cool nights about April 1st, but no frost and the next ten days were entirely summerlike.

The result was that by April 15th vegetation was as far advanced as it is usually in late May. and was growing very rapidly without having received any check whatever. Fruit trees were in full bloom or a little past their prime. Many of the forest trees were in leaf, others were just leaving out and growing rapidly. Much of the earliest herbaceous vegetation was through flowering (e.g. *Sanguinaria, Hepatica*) and developing its fruits, while many of the slightly later herbs were at the maximum of flowering.

On April 15th it began to freeze a little before midnight and about sunrise of the 16th reached a temperature of -2.7° C (27° F.). Somewhat less intense frost occurred on the two following nights. During the intervening days the temperature rose a few degrees above freezing. The weather was cloudy and on the afternoon of the 16th about two inches of wet snow fell, remaining on the ground and on vegetation until the morning of the 18th. This period, April 15th to 18th, will be spoken of collectively as the "first frost." Nearly all the damage to vegetation occurred during the night of April 15th. The slightly higher temperature of the following nights in connection with the covering of snow produced almost no injury to vegetation which had survived the frost of the first night.

By April 19th summer conditions were again established, and the daily maximum temperatures for the next few days ranged from 20° C to 26° C (68° to 80° F). On April 22nd the temperature began to fall very rapidly, passed the freezing point about five o'clock in the afternoon, reached a minimum temperature of -7.2° C (19° F) early in the morning of April 23rd and remained below freezing until the morning of April 25th—over sixty hours of continuous freezing. At the time of the lowest temperature, on April 23rd, a northwesterly gale was blowing, so that the temperature was very uniform and there were no pockets of warm air as there sometimes are during cold but quiet nights. This period of freezing, from April 22nd to 25th, will be spoken of collectively as the "second frost." After April 25th the weather became mild again, but was cooler than usual for about six weeks and there were several light frosts after May 1st.

It will be seen from this account that vegetation in a condition of active growth was subjected to two periods of prolonged cold, the first with a minimum temperature of -2.7° C, the second with a minimum temperature of -7.2° C. The effects of the freezing were noted in the case of a large number of species both of woody and of herbaceous plants.

Mechanical Injury Resulting From Low Temperatures.—In both frosts it was found that much mechanical damage was done to plants, often when they were otherwise quite frost-hardy. This mechanical damage was mainly of two kinds. (1). It is a well-known fact that just before freezing occurs in plant tissue much of the water of the cell sap is secreted into the intercellular spaces. The resulting loss of turgidity allowed the young and succulent twigs, often loaded with heavy foliage, to bend sharply and in many cases the vascular tracts were unable to stand the strain and breaks occurred. This damage was greatest in the case of somewhat succulent herbaceous plants, such as peonies and lilies and such native plants as *Trillium grandiflorum.* In many cases, also, the young twigs of woody plants suffered in the same manner. Sometimes when no actual break occurred the bending was so great that the plant was later unable to straighten the twigs and many curiously distorted shoots resulted. It was estimated after the first frost that fully half the damage done to

TABLE I. TE

Celastrus scandens ......
Celtis occidentalis ....
Fraxinus lanceolata .....
Gleditschia triacanthos ...
Juglans cinerea ....
Parthenocissus quinquefo
Quercus coccinea ......
Quercus macrocarpa ....
Quercus platanoides ....
Robinia pseudacacia ....
Rhus hirta ....
Vitis vulpina ....
Weigelia ....

(See Table III), and fully 50 per cent. of the native herbs, there was no effect visible a few days after the frost, despite the fact that they were in active growth at the time of the frost.*

TABLE I. TENDER TREES AND SHRUBS. NEW GROWTH KILLED BY FIRST FROST.

	Condition Previous to Freezing.		Remarks
	Leaves and Twigs.	Flower Buds and Flowers.	
Celastrus scandens	Leaves fully out, growth 20 cm. or more.		
Celtis occidentalis	Growth for the year well along, leaves 1-3 cm. long.	Flowers all out and pollinated.	After second frost the cambium appeared black on 1st and 2nd year shoots, the 3rd year shoots also injured. On May 3rd latent buds came out on last year's and older twigs
Fraxinus lanceolata	Leaves just unfolding.	Flowers fully out.	On May 3rd the cambium appeared black 15 cm back from the tips of the branches. New buds started from base of last year's growth.
Gleditschia triacanthos	Leaves beginning to unfold.		On April 28th terminal buds and many accessory buds were showing up.
Juglans cinerea	Buds opening.	Flowers just opened.	
Parthenocissus quinquefolia..	About half of the year's growth made.		
Quercus coccinea	Leaves just unfolding.	Staminate catkins out; pollen not discharged.	The one-year-old acorns not injured.
Quercus macrocarpa	Leaf buds open and leaves about 4-5 cm.	Staminate flowers fully out; pollen not discharged.	Some late buds not destroyed until second frost, cambium turned black on one-year-old twigs.
Quercus platanoides	Leaves unfolding.	Not noticed.	
Robinia pseudacacia	Leaves just starting.		Leaves and opening buds killed completely by the first frost.
Rhus hirta	Leaves unfolding.		The leaves and buds just breaking out, all killed by the first frost.
Vitis vulpina	Leaves unfolding.	Buds exposed.	
Weigelia	Three pairs of leaves unfolded.		Last year's shoots killed by the second frost.

vegetation in general was of this type. (2). During the very severe freezing of April 23rd succulent parts of plants froze absolutely solid and became very brittle. In this condition many of them were snapped off by the high wind.

The amount of mechanical damage in the case of any plant was quite independent of the actual frost-hardiness of the protoplasm. Of course it was most conspicuous in those plants which received comparatively little direct injury from the low temperature. Both sorts of mechanical injury, particularly that of the second kind, were much greater in exposed than in protected situations. The lilac bush (Fig. 1) exhibits the effect of direct exposure to the wind during the morning of April 23rd. Scarcely a leaf or young twig remained alive on the windward (northerly) side of the bush.

Direct Effects of Low Temperature. Relative Hardiness of Different Species and Different Parts of Plants.—As was to be expected, different plants showed to very different degrees the power of surviving the low temperature. Many had all their new growth killed or severely injured by the first frost. These included about 24 per cent. of the native trees and shrubs (See Table I). With these were some exotic herbaceous plants but almost no native herbs. A larger number escaped with little injury from the first frost but were severely injured by the second—about 30 per cent. of native woody plants (See Table II), and a somewhat smaller proportion of native herbaceous vegetation. In many cases the mechanical damage during the second frost was so great that it was impossible to determine whether or not the protoplasm of the plant was frost-hardy to the extent of enduring the temperatures that then obtained. It appears evident, however, that irrespective of this mechanical injury many plants are able to endure 2.5 degrees (C.) of freezing but are killed or severely injured by an additional five degrees. Many plants showed comparatively few ill effects resulting directly from the cold. In about 10 per cent. of the woody plants examined (See Table III), and fully 50 per cent. of the native herbs, there was no effect visible a few days after the frost, despite the fact that they were in active growth at the time of the frost.*

In many plants only certain parts were affected. In general flowers, flower-buds and fruit proved less hardy than the vegetative parts of the same plants. Also, parts in active growth and those well filled with water were less hardy than the same organs in a less active condition. Thus, leaf-buds which had scarcely started were more hardy than those which had progressed further, half-grown leaves were very tender, while the fully expanded and ripened leaves were more hardy again. In the same manner opening flower-buds and the expanded flowers were more tender than either small buds or ripening fruit. Several peculiar cases of selective killing were noted. Thus, in several plants the pistil was killed within an otherwise uninjured flower-bud. This happened in nearly all the unopened buds of the apple. Often the flowers afterwards expanded as if uninjured. In *Sanguinaria* the ovules were killed within the developing fruit, while the pericarp was uninjured and continued to grow for several weeks.

Relative Injury to Different Types of Vegetation. (1). *Herbaceous Vegetation.*—Native perennial herbaceous vegetation suffered surprisingly little damage. Less than 50 per cent of these plants were hurt at all, and in these cases injury was mainly mechanical, or confined to flowers, the edges of unfolding leaves, ripening fruit or similar tender parts. By the middle of May native herbaceous vegetation had an entirely normal aspect. That it had received no serious check was shown by the fact that until late summer it remained several weeks ahead of the usual seasonal development. This immunity to injury was not due to any great extent to the more protected position of the herbs but to an actual hardiness far in excess of that shown by woody plants. Exotic garden plants did not possess it to any great extent. It was more notable among the plants which form the vegetation of the exposed prairies than in the case of the comparatively sheltered herbaceous undergrowth of the forest. In fact, nearly all of the native herbaceous plants which were injured were among those growing in the latter situation. As the actively growing parts of herbaceous plants are not *per se* any more capable of withstanding hard

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*About 5 per cent of trees and shrubs were still in a dormant condition, and were uninjured.

Acer negundo ..
Acer saccharinum
Betula papyrifera ...
Cornus amomum.
Cornus alternifolius..
Ostrya virginiana....
Populus deltoidea
Prunus

TABLE II. HALF HARDY SPECIES OF TREES AND SHRUBS

	Condition previous to Freezing		Condition of Vegetative Parts after Freezing				Condition of Flowers		Remarks
			Results of First Freezing		Results of Second Freezing				
	Leaves and Twigs	Flower Buds Flowers, etc.	Leaves	Twigs	Leaves	Twigs	After First Freezing	After Second Freezing	
Acer negundo ..	3-5 pairs of leaves unfolded, oldest nearly full grown	Past flowering.	About half of the leaves killed.	Little or not at all injured.	Practically all killed.	Tips of shoots killed, rest not injured.	Fruit ? ?	Fruit killed.	Many twigs recovered.
Acer saccharinum	Leaves unfolding, first pair nearly full grown.	Flowers all past, fruit nearly mature.	Some leaves badly frozen.	Not injured.	Completely killed	Considerably injured, mostly mechanical.	Fruit uninjured.	Fruit killed.	Buds at the lower nodes of the uninjured shoots started growing.
Betula papyrifera ...	Leaves unfolding about 2 cm. long.	Out and pollinated.	Not injured.	Not injured.	About half of the leaves killed.	Exposed internodes injured.	Not injured.	Killed.	The one year shoots in many cases appeared injured, not permanent.
Cornus amomum.	Just opening the first pair of leaves	Not out.	??	??	Completely killed	Not out.			
Cornus alternifolius..	Leaves nearly out, oldest blades 4-5 cm.	Flower buds exposed.	Not injured.	Not injured.	Some leaves killed, others on the same shoots unharmed.	Those most exposed injured and a few killed.	Buds not injured.	Many buds killed others apparently not hurt.	
Ostrya virginiana....	Leaves unfolding, oldest about 3 cm long.	Flowers out.	Not injured.	Not injured.	Badly frozen, a few leaves surviving.	Nearly all exposed internodes killed.	Probably not injured.	All killed in exposed places.	
Populus deltoidea	Nearly full season's growth of leaves.	Past flowering.	Old leaves not injured, young leaves killed.	Probably some killed at the tips.	Mostly killed.	Killed except at the base, 2-3 internodes not affected.	Fruit not injured.	Killed.	Many young twigs were killed a few resumed growth at tips, a few of the first leaves were not killed.
Prunus virginiana....	Completed year's growth and forming terminal and lateral buds.	Buds not open.	Not injured.	Not injured.	Some leaves especially on terminal twigs were killed, others not hurt.	Some terminal shoots killed.	Buds not injured.	Buds apparently uninjured.	Cortex of older twigs for some time appeared affected, recovered later.
Salix cordata....	Leaves fully out.	Fruit nearly ripe.	Not affected.	Not affected.	About one half of the leaves killed, especially young ones.	Outer parts mostly killed.	Fruit not injured.	Some fruits shedding cotton without seeds, others probably are unharmed.	
Sambucus pubens	4-5 pairs of leaves, oldest full grown	In full bloom.	Partly injured but reviving.	Not injured.	Mostly killed.	Damage severe, mostly mechanical.	Slightly injured.	Killed.	A few uninjured shoots resumed growth.
Spiraea van Houtei.......	Twigs out about 2 cm. leaves unfolding.	Flower buds exposed, not large.	Slightly injured.	Not injured.	Killed.	Almost all killed.	Flower buds mostly killed.	Killed entirely.	New growth produced occasional flowers.
Staphylea trifolia	Growth well advanced, 3-4 pairs of leaves.	Just beginning to blossom.	Not injured?	Not injured.	Most of the first leaves injured.	Not injured.	Flower buds not injured but open flowers probably affected.	Flowers and the flower buds mostly killed.	
Syringa vulgaris.	Full growth of the season, leaves nearly full grown.	First buds just opening.	Some leaves much injured.	Not affected.	Nearly all killed.	Mostly uninjured except sometimes last internodes.	Buds not much injured.	Flowers and buds all killed.	After the second frost many flower buds still appeared uninjured. They remained unopened and finally died.
Tilia americana..	Leaf buds just opening, largest leaves 2.5 cm. long.		Some leaves injured along the edges.	[illegible]	Oldest leaves frozen around the edges, younger exposed leaves killed.	Slightly injured, not permanent.			Buds unfolded at the lower internodes of the new shoots.
Ulmus americana	Very variable, some shoots just starting, others 15 cm. long.	Fruit nearly ripe.	Some leaves injured along the edges.	Not injured.	Mostly killed except where just unfolding.	Very variable, exposed internodes mostly killed.	Fruit not injured.	Fruit mostly killed.	On some trees in exposed situations the one-year old twigs were injured or killed.

frosts than any other vegetable tissues, it appears that our herbaceous vegetation, and especially that of the prairie, is the survival from a long period of natural selection along these lines. In herbaceous plant societies the advantage gained by a plant which is able to survive such an experience over one which is killed back to the ground and has to begin the season's growth anew, is very great and this advantage has led to the almost complete extermination of frost-tender herbs.

(2). *Woody Vegetation.*—Trees and shrubs, on the other hand, suffered etxensive and more or less permanent injury. The following figures are based on the examination of about 50 species including a few common cultivated ones. The omission of the latter would make no appreciable difference in the results. Less than 15 per cent escaped injury. In about 45 per cent the damage was limited to the leaves with occasional mechanical injury to the young twigs. In these the damage ranged all the way from a slight injury to a few leaves up to almost complete defoliation. In about 30 per cent the young twigs were much injured or wholly destroyed, and in 10 per cent the old woody twigs also were killed or injured—sometimes those of several years' growth (e.g. *Quercus macrocarpa, Celtis*).*

The greater tenderness of our woody vegetation as compared with our herbaceous plants is to be explained as due to two factors. (1). Between woody plants there is a less immediate competition for light than among herbs. No tree can greatly overshade its neighbors by developing a few weeks ahead of them as may easily happen in the case of herbaceous plants. There has been, therefore, a much weaker tendency toward the elimination of frost-tender trees than of frost-tender herbs. It is obvious, however, that any frequent repetition of conditions as severe as those of April, 1910, would permanently check the growth of some of our more tender trees and would eventually lead to their disappearance from our flora. (2). The general distribution of our forest flora indicates that it has migrated from the south and east and conditions of the sort which obtained in Minnesota

*In *Celtis* all the new growth was destroyed by the first frost. After the second frost the cambium and adjacent cells appeared black and watery in the woody twigs of 1909, 1908 and, for the most part, in those of 1907. Actual death of the twigs was largely confined to the distal part of those of 1909. Enough cambium cells remained alive in the older twigs to start a new growth, but sections taken in December, 1910, show a ring of black undeveloped dead cells in the midst of the wood for the year.

in 1910 appear to be of less frequent occurrence in the parts of the country from which these plants have migrated. This is the probable explanation also of the comparative tenderness of the herbaceous undergrowth of the forest—plants which have undoubtedly migrated along with the forest trees.

Recuperation of the Frozen Plants.—Recuperation from the effects of the frosts was often a slow process and much of the woody vegetation had an abnormal appearance all summer.

In cases where the injury was slight growth was but little checked and proceeded normally. When there was extensive defoliation any leaves which escaped often grew to unusually large size, and new growth developed in one of several ways. (1). As would be expected many latent buds on the woody twigs and branches sprang into activity. This was more or less true in all cases of severe injury and was the only possible method of recuperation when all of the new growth had been killed. In some cases these buds started to grow on twigs which themselves had been so severely injured that they later proved unable to support the new growth. This then withered and other latent buds on still older twigs were brought into growth.* (2). When the young twigs were partially but not entirely killed, shoots frequently appeared in the leaf axils of the lower nodes of the current season's growth. In some cases these shoots appeared directly without the production of any scaly buds. In other cases buds with a few scales formed and quickly started into growth. As a result of this the season's growth consisted of a main axis with numerous lateral twigs giving the trees a somewhat fasciated appearance. (3). When the injury was confined to the leaves the terminal bud often continued to develop until a sufficient number of new, leaf-bearing nodes were formed. These long switch-like branches were often considerably longer than the normal growth for one season. Some trees employed one of these methods. some another and some used any one of the three, according to the extent of the injury affecting the particular branch. In a few cases recuperation was very slow—it was after midsummer before

*Many hackberry and ash trees and some oaks showed this effect. It was probably due to the killing of the phloem and cambium of the old twigs.

TABL

Acer rubrum
Acer saccha
Berberis vul
Cornus alter folius .....
Corylus ame cana ....
Euonymous atropurpureu
Hicoria mini:
Juniperus munis .....
Juniperus vi iana ....
Malus Ioens
Philadelphus coronarius ..
Physocarpus opulifolius ..
Picia Marian
Prunus americana ..
Rubus occi-dentalis ....
Salix fluviat
Symphoricar racemosus .

TABLE III. RELATIVELY HARDY SPECIES OF TREES AND SHRUBS,—VEGETATIVE PARTS MAINLY UNINJURED BY FIRST FROST, INJURY BY SECOND FROST LARGELY MECHANICAL.

	Condition Previous to Freezing		Condition of Vegetative Parts after Freezing	Condition of Flowers, Fruits, Etc.		Remarks
	Leaves and Twigs	Flower Buds and Flowers		After First Freezing	After Second Freezing	
Acer rubrum	Leaves unfolding, first pair nearly full grown.	Past blooming, fruit nearly mature.	Some leaves badly injured by first frost, all killed by second one	Fruits uninjured.	Completely killed	Some young shoots considerably injured but mostly mechanical.
Acer saccharum.	Leaves unfolding. Dwarf shoots	All out and pollinated.	Exposed leaves slightly injured.	Apparently not injured.	??	
Berberis vulgaris	fully out.		Some leaves killed, others injured			No check to normal development.
Cornus alternifolius	Nearly leaved out, oldest blades 4-5 cm.	Flower buds exposed.	Some leaves killed, others not harmed	Buds uninjured.	Many buds killed, others uninjured.	Some of the most advanced young shoots injured, others killed.
Corylus americana	Leaves about 4 cm along.	Completely out and pollinated.	Youngest leaves nipped, older ones uninjured	Fruit uninjured.	Uninjured and developing.	
Euonymous atropurpureus	Full growth for the year except terminal buds.	Buds just opening.	Some leaves killed, others not affected	Buds not affected.	Buds not injured.	Young shoots not touched.
Hicoria minima.	Buds just beginning to open.	Not out.	Some of advanced buds injured	Not out.	Not out.	
Juniperus communis	Leaf buds just opening.	Unopened.	Some young growth injured.	Not affected.	Not affected.	
Juniperus virginiana	Just beginning to grow.	Staminate flowers, pollen discharged	Foliage slightly injured; shoots affected	??	??	Flowers probably injured by the frost.
Malus Ioense	Many leaves full grown.	Buds unopened.	Some of the older leaves killed	Buds uninjured.	Petals on some; flowers injured.	Young shoots uninjured.
Philadelphus coronarius	Growth well along, 3-4 pairs of leaves.	Buds just opening.	Many leaves killed by second frost	Uninjured.	Only slightly injured.	Considerable mechanical injury to shoots.
Physocarpus opulifolius	Almost in full leaf.	Buds just opening.	A few leaves killed	Not affected.	Not affected.	
Picia Mariana	Buds opening, some 2 cm. long.		Few shoots dead, uncertain whether caused by freezing			No check to normal growth appeared by April 28th.
Prunus americana	Just beginning to unfold.	Flowers mostly out.	Leaves injured by first and killed by second frost.	Flowers nearly all killed.	A very few buds apparently not injured.	Young shoots on exposed side of tree killed, on protected side not much injured.
Rubus occidentalis	Nearly full growth of shoots.	Just opening.	Foliage considerably injured.	Not injured.	Apparently uninjured.	Mechanical injury to shoots.
Salix fluviatilis.	Nearly full foliage.	In blossom.	Some leaves killed	Not affected.	A few flowers killed.	
Symphoricarpos racemosus	In full foliage, leaves nearly full grown.		Slightly affected by first frost and in exposed situations upper leaves killed by second.			Damage largely mechanical.

the cottonwood trees had any foliage other than the few very large leaves which had survived the frost.

The various methods of recuperation can be readily seen in the photographs of lilac (Fig. 2) and basswood (Fig. 3) branches taken about a month after the frost.

When the flowers or flower-buds were destroyed, the plant usually produced no flowers during the season, but in some cases (e. g. grape, both cultivated and native, *Spiraea van Houttei*) a new crop of flower-buds appeared on the new growth produced after the frost. In some cases the flowering habits of the plant were completely disturbed. Thus *Ribes aureum* produced curious abnormal inflorescences (long racemes with leafy bracts terminating the young twigs) throughout the late summer and until hard frost in late October.

Summary. (1). Prolonged solid freezing will injure many plants and parts of plants which are not hurt by 2.5 degrees (C) of frost. (2). Mechanical damage from loss of turgidity and brittleness of frozen members is great. (3). Hard freezing is far more destructive to our native woody plants than to our herbaceous vegetation. (4). Woody plants recover from hard freezing very slowly and produce very abnormal growth for the season in which it occurs.

EXPLANATION OF PLATE.

PLATE XXIII.

Fig. 1.—A group of lilac bushes (*Syringa vulgaris*) on the University Campus. The windward (northerly) side was fully exposed and the leaves and twigs were killed. The leeward side was but slightly affected.

Fig. 2.—Twig of lilac taken about a month after second frost, showing method of recuperation. A number of injured leaves still remain attached.

Fig. 3.—Twig of basswood (*Tilia americana*) about a month after second frost. A bud near the base of the current year's growth is unfolding; the large leaf is one that survived the frost.

Fig. 1

Fig. 2

Fig. 3

PLATE XXIII

NOTES ON THE SPECIES OF LIAGORA AND GALAXAURA OF THE CENTRAL PACIFIC.

Frederic K. Butters.

During the past nine years it has been my privilege to examine large collections of specimens of the genera *Liagora* and *Galaxaura* from the islands of the Pacific ocean. The largest of these collections was made by Professor Josephine E. Tilden in the Hawaiian Islands during the summer of 1900. A few specimens of this collection have been distributed by Miss Tilden in her Centuries of American Algae. Other collections were made by the United States Fish Commission from the Hawaiian Islands proper and from Bird Island and the Island of Laysan, northwest of that group, and by Miss Tilden from the Island of Tahiti. I have also examined all the material of these genera in the herbarium of the university which was collected in the central part of the Pacific, notably some collections by A. A. Heller from the Hawaiian Islands.

The collections of Miss Tilden and of the Fish Commission are preserved in formaldehyde and so admit of much closer and more accurate study than in the case of ordinary dried material. Specimens of all the species discussed below are deposited in the collections of the Botanical Department of the University of Minnesota.

I wish to express my thanks to Miss Tilden for placing these collections at my disposal and for many useful suggestions during my study of them, and to Miss Charlotte Waugh for preparing the drawings upon which the value of such descriptions as the following must largely rest.

There are in the collections examined thirteen distinct forms of the Genus *Liagora* and twelve of *Galaxaura,* besides a few fragments which are probably distinct but are too fragmentary to warrant any attempt at complete description. The question of the limitation of species is very troublesome in both genera and particular-

ly so in *Liagora.* Some forms can often be distinguished only by microscopic characters, while in other cases forms microscopically very similar can be distinguished by differences in habit, branching, incrustation and the like. Botanists have differed greatly as to the value of the various distinctions and only long work with the living plants will probably settle the question. To make the matter worse, nearly all the older descriptions are entirely inadequate, many of the illustrations which have been published are, to say the least, insufficient and difficult to identify, and dried herbarium material of these genera is very unsatisfactory for microscopic work.

In the genus *Galaxaura* the monograph of Kjellman (Om Floridé-Slägtet Galaxaura dess Organografi och Systematik, F. R. Kjellman, Stockholm, 1900) gives an admirable basis for taxonomic work, and greatly simplifies the treatment of this genus. Agardh's corresponding work on *Liagora* (Agardh, J. G. De differentiis in structura frondis, quae in diversis Liagorae speciebus observantur. Analecta Algologica III.: 96, 1896), is not so satisfactory, largely owing to the entire lack of illustrations.

In view of these facts it has seemed best to describe fully, and in most cases with illustrations, all the forms which I have examined, with the exception of a few well known species of wide distribution, in the hopes that this treatment may lead to further study of these interesting and too little known genera. It has appeared necessary to describe a number of these forms as new and this has seemed more desirable than an attempt to identify them with the numerous species described in most cases from distant parts of the world, and with such slight attention to detail as to be practically *nomina nuda*.

Key to Sections of Liagora.

I. Decalcified frond gelatinous; central cylinder composed of large primary cylindrical filaments and smaller filaments which surround these and penetrate among them; cortical filaments of elongated cells contracted at the nodes, ending in much branched heads of moniliform cells; antheridia small. **Eu-Liagora** J. Ag.

II. Decalcified frond soft mucilaginous; central cylinder composed of large primary cells which are close packed and often angular and of small cylindrical filaments, which surround the larger filaments and only occasionally penetrate between them.

1. Cortical filaments as in Eu-Liagora. **Corymbosae** sect. nov.

2. Cortical filaments of cylindrical cells less freely branched than in Eu-Liagora; antheridia forming large and conspicuous heads.

Goralia J. Ag.

Section 1. **Euliagora,** J. Ag. Anal. algol. 3:99. 1896.

Liagora leprosa. J. AG. Alg. Liebm. 8. 1847. Tilden. American Algae. Cent. V. no. 417. 1901.

Frond dichotomously decompound, rotund-corymbose, terete, flattened below on drying, covered with a mealy incrustation, with obtuse, patent apices, green when young.

On rocks at low tide. Laie Point, Koolauloa, Oahu. June 18, 1900. (J. E. T. 1005); Waianae, Oahu. May 26, 1900, (J. E. T. 862); Hanalei, Kauai. July 26, 1900, (J. E. T. 1221).

The frond is small, 3-4 cm. high, .75 mm. thick at base, repeatedly dichotomous without lateral proliferations, covered with a pulverulent coat of lime. The central cylinder is somewhat firm and narrow throughout, composed of cylindrical filaments of two sizes. The cortical branchlets arise from the larger central filaments and are about 225 mic. long. They appear to be somewhat shorter stalked than in the type of the species. They are often dichotomous at the summit of the basal cell. The basal cell is long-cylindrical, 8-9 x 30-40 mic., the next somewhat longer and narrower with gradual transition upward to the almost spherical cells of the corymbose head (about 9x10 mic.) which usually bear several minute cells about 2 mic. in diameter. Cystocarps are abundant, sub-prominent, often almost completely covering a branch. The involucre is scant, resembling the vegetative cortical branchlets and frequently, like the latter, produces small medullary filaments.

Specimen J. E. T. 862 A. Waianae, Oahu, May 26, 1900. One small plant, 2 cm. high and .5 mm. thick at base, resembling the above but with the cystocarps deeply sunk among the cortical branchlets, furnished with an abundant involucre of cylindrical, simple or sparingly branched filaments.

Specimen J. E. T. 1005. Laie Point, Koolauloa, Oahu. In the same collection with *L. leprosa*. A fragment resembling *Liagora leprosa* but with numerous lateral proliferations. Structure similar but the cystocarps not prominent.

Liagora pulverulenta AG. Sp. 296. J. G. Ag. Sp. Gen. et

Ord. Floridearum. 2:427. 1852. Kütz. Tab. Phyc. 8:42. pl. 89. 1858.

PLATE XXIV. FIG. 1.

Frond terete, flattened below on drying, subcanaliculate, above terete, dichotomous, subpinnate, with very numerous lateral proliferations covered with a mealy, somewhat uniform crust of lime; apices divaricate, obtuse, purplish when young.

Two collections. Tahiti, Society Islands. September, 1910. (J. E. T.)

The frond is small, 4-6 cm. high, .75 mm. thick at base, with the principal branches about .5 mm. thick. It branches repeatedly in a dichotomous manner with short internodes (3-8 mm.) from which spring very many lateral proliferations which may be simple or forked. The calcareous incrustation is somewhat mealy, becoming firmer in the older parts of the frond, but not forming a continuous smooth layer. The tips are free from lime for a distance of one or two mm. The central cylinder is somewhat firm and thick in the older parts of the frond, composed of terete filaments of two sizes; the larger are composed of cells about 200-225 mic. long and 10 mic. wide at the lower end, over 20 mic. wide about the middle, and 15-17 mic. wide at the top where the filament branches, giving off one of the cortical branchlets. The smaller medullary filaments are cylindrical, about 4 mic. in diameter, little branched. They arise first from the lower cells of the cortical branchlets, later from nearer the top and even those just below the corymbose summit. The cortical branchlets are 250-400 mic. long, several times dichotomous near the base. The basal cell is nearly cylindrical, about 10x35 mic. Those just above it are slightly longer and narrower, becoming elliptical towards the summit of the branchlet, expanding suddenly into the several times divaricately di- or trichotomous corymb of short ellipsoidal cells (about 4-6 mic.), the outer ones often bearing a very small conical tip cell (2x3.5 mic.) The cystocarps are large with a scanty involucre of the tips of the vegetative filaments.

Liagora tenuis J. Ag. Anal. Algol. 3:101. 1896. De Toni. Syll. Algar. 4:89. 1897.

PLATE XXIV. FIG. 2.

Frond terete, dichotomously decompound, subcorymbose, with obtuse apices, the whole lower part covered with a continuous calcareous crust marked with scattering denuded dots (cystocarps),

central cylinder translucently thin, its diameter scarcely equalling the length of the fascicles, fascicles vertical, below very slender, hyaline, above distantly dichotomous with acute angles, at the top terminated by a corymb of short branches, at the apex of the branches of the frond forming a dense cushion.

Waianae, Oahu. May 26, 1900. (J. E. T. 861.)

It is with some hesitation that I include this specimen in the above species. The Hawaiian specimens are small, 1.5-3 cm. high, .5-.75 mm. in diameter, dichotomously branched at intervals of 2-8 mm., sometimes appearing pinnate by the unequal development of the two branches of a dichotomy. With the exception of the obtuse tips of the branches the frond is completely covered with a solid crust of lime, which is, however, punctate with uncalcified dots, the cystocarps. The whole frond is very brittle and fragile.

The central cylinder is composed in the young branch, of somewhat closely packed large filaments, while in slightly older branches smaller filaments intervene between these, and also surround the whole central cylinder. The central cylinder remains thin, being about .3 mm. in diameter in mature branches. It is somewhat firmly gelatinous. The cortical branchlets cohere in a dense pulvinate tuft at the apex of the branch. Below they are somewhat widely separated. The lowest cells in the branchlets outside the central cylinder are 8-10 mic. in diameter and about four times as long. Upward the branches are several times dichotomous with narrow acute angles. At the summit they form a somewhat loose corymb of moniliform filaments of obovate cells, the distal cells averaging 5x10 mic. The cells towards the base of the corymbose head are often three times as long and twice as wide as the terminal cells. In the older parts of the frond the latter not infrequently disappear. Numerous cystocarps are present with the involucre little marked and resembling the ordinary vegetative filaments of the frond.

Liagora maxima sp. nov.

Tilden, American Algae. Cent. V. no. 418. 1901. *(L. decussata.)*

PLATE XXIV. FIG. 3-5.

Fronde tereti, pinnatim paniculata ad 40 cm. alta inferne 1-1.5 mm. lata, a basi sursum parum attenuata ramos inferiores axi principali similes et eundem paene aequantes superiores breves, obtusissimos clavatos quasi pedunculatos gerente, crusta farinacea instruc-

ta quae aut de ramis ultimis deest aut in his ramis levis est et ramulis corticalibus tegitur; axile strato (in emollita) cartilagineo, in partibus ramorum inferioribus et in frondis axi fasciculis corticalibus decedentibus exposito, filis aliis latioribus aliis tenuioribus intertextis composito, filis tenuioribus primum paucis, paulatim pluribus et in partibus frondis veterioribus plurimis; strato corticale ramorum ramulis verticaliter exeuntibus inferne cellulis angustis cylindraceis instructis, supra axillis acutissimis subfrequenter dichotomis, superne in corymbos terminales filorum ultimorum bitricellulatorum conglutinatorum exeuntibus cellulis breviter ovatis composito; cystocarpiis involucro filorum ramulis ultimis strati corticalis consimilibus circumdatis; antheridiis ad cellulos ultimos ramulorum corticalium elongatos fasciculis parvis factis.

Attached to rocks on sandy beach at low tide, on a rocky peninsula, two miles north of Waianae, Oahu. June 12, 1900. (J. E. T. 983, 1564.) The species differs from *L. decussata* in the granular incrustation, the clavate form of the smaller branches, and in the size and form of the cells of the cortical branchlets. It apparently is closely allied to *L. orientalis* J. Ag. and may be the form mentioned by Agardh (Anal. Algol. 3:100) as collected in Japan by the Wright expedition and in Australia by J. B. Wilson.

The abundantly dichotomous cortical branchlets cover only the distal parts of the branches. They consist below of elongated cylindrical cells about 8 mic. wide, and above of shorter and more ovate cells, the terminal cells averaging 9-10x14-15 mic. In antheridia-bearing branches, however, the terminal cells are elongated obovate, 4-6x10-20 mic. The transition from long cylindrical to ovate cells is gradual. Branching seldom occurs at every cell even in the terminal corymbose portion of the branchlet and the ultimate filaments are usually unbranched for the last two or three cells. These cortical branchlets are deciduous in the older parts of the frond and are then replaced by short filaments often unbranched and usually only 3-6 cells long. This occurs everywhere along the main axis of the frond and in the basal parts of the branches. Where this occurs the calcareous crust is exposed, when not itself deciduous, while in the younger parts it is enclosed as a granular mass among the cortical branchlets the corymbose tips of which project above it, so that the lime is not evident in dried material.

The type material has been distributed by Miss Tilden under the name *Liagora decussata* Mont, in American Algae, no. 418.

Liagora intricata sp. nov.

PLATE XXIV. FIG. 6.

Fronde parva, dure gelatinosa, dichotome furcata, ramis saepe coalescentibus intricata, crusta calcarea continua transversim striata (in exsiccatione rugosa) obtecta apicibus decalcaratis conspicuis obtussisimis (exsiccatione acutis factis); strato axile duro cartilagineo, filis teretibus, cylindraceis composito, et minoribus et majoribus, his ad 15 mic. crassis parietibus crassissimis, illis ad 4 mic. crassis, ex filis corticalibus orientibus et in stratum exile redeuntibus; ramulis corticalibus brevibus, duplo seu tripolo dichotomis, corymbum abruptum ferentibus cujus cellulae ultimae obovatae ad 18 mic. longae, 10 mic. crassae sunt, cellulis sub corymbum minutorum binorum ex cellulis ultimis atque praecipue penultimis ramulorum corticalium orientum; cystocarpiis maturis mihi ignotis. filis plurimis rhizoideis ferentibus; antheridiis catenulis cellulorum

Tahiti, Society Islands. September, 1910. (J. E. T.)

Diamond Head, Oahu. (A. A. Heller no. 2285a) (as *Galaxaura rugosa.* [Soland.] Lam. var. *attenuata* n. var.) The "type material" in the herbarium of the University of Minnesota agrees with the above described Tahitian *Liagora*.

This species has a somewhat stout but short and much branched frond. The branches are intricately woven together and often grow fast to one another at the points of contact. It has a very firm cartilaginous texture, much like that of some *Galaxauras*. The limy incrustation is continuous, not very firm in the material from Tahiti (preserved in formaline), but in the dried Hawaiian material firm and rugose. The central cylinder becomes stout and is characterized by the almost cylindrical form and exceedingly thick walls of the larger filaments. These filaments are 12-17 mic. in diameter, increasing only about 2 mic. towards the distal end of each cell. Their cell contents are only about 2 mic. in width. These cells bear the cortical branchlets, which are only about 200 mic. long. The first two or three cells of a cortical branch are narrowly cylindrical and thick walled, about 8x35 mic. The next cells are elongated elliptical, about 10x30 mic., the terminal ones obovate, about 12x14 mic. These filaments are commonly forked at the summit of each of the first two or three cells (in these branchings

one side of the dichotomy appears slightly lateral upon the other), once or twice about half way to the summit. and abruptly several times at the summit, forming a small compact corymb. All the proximal cells, and in old parts of the frond the median cells also. give off rhizoidal-like branches about 5 mic. in diameter, which grow down into the central part of the frond and form the small filaments of that region. Antheridia are of the usual type found in species of *Eu-Liagora*. Nearly all the antheridial filaments are borne on the penultimate cells of the cortical filaments. Cystocarps appear to be very rare. No mature ones have been seen, but a few young ones in the Tahitian material have the ordinary structure of the genus.

Liagora sub-paniculata sp. nov.

PLATE XXIV. FIG. 7.

Fronde irregulariter dichotoma per ramis binis inaequaliter crescendis quasi paniculata ad 10 cm. alta, 1-1.25 mm. lata ad apices conicos obtusos parum attenuata, paene ad apices ramorum calcis incrustatione primo pulverulenta deinde continua annulata rugosa instructa; strato axile molli elastico-gelatinoso filis cylindraceis et latioribus et angustioribus laxe intertextis composita in partibus vetustioribus frondis quam semidiametro frondis latiore, ramulis corticalibus laxe tecto qui inferne cellulis cylindraceis superne elongatis instructi et parce furcati capitula corymbosa cellulorum ovalium seu globosorum subiter ferunt; cystocarpiis conspicuiis ut punctis subprominentibus decalcaratis, magnis parce involucratis.

North of Hotel, Waianae, Oahu. May 26, 1900. (J. E. T. 863, 864); Waianae, Oahu. June 12, 1900. (J. E. T. 1564 B); Kauai, June 23, 1902. 18-41 fathoms. S. For. Co. R. (U. S. Fish Com. 4023A.)

The frond is dichotomously branched, but as one of the branches of a dichotomy is usually retarded in its growth it comes to have a subpinnate, paniculate aspect. The incrustation of lime varies considerably, being at first pulverulent and remaining so in some small specimens, but in others and in all large specimens becoming continuous and roughly rugose. In outward appearance agreeing closely with *Liagora rugosa,* it has, however, the internal structure of the sub-genus *Eu-Liagora*. The large medullary filaments are numerous, thick-walled, very prominent in a surface view of a slightly crushed branch, cylindrical or somewhat larger toward the

upper end of each cell. They average 28 mic. in diameter. The proportion of smaller medullary filaments varies in different specimens. The medulla, at first small, may come eventually to occupy rather more than half the diameter of the frond. The cortical branchlets are borne on the larger medullary filaments or in some cases on the successive nodes of comparatively short lateral branches of the larger filaments. The cortical branchlets are characterized by the elongated cylindrical cells of the median portion (8x40 mic.), becoming somewhat shorter and more ovate above and by the abrupt terminal corymbs of short oval cells, the distal cell being almost spherical, 8-10 mic. in diameter. At the apex of each branch of the frond the cortical branches form a dense pulvinate conical mass. Elsewhere they but loosely cover the medullary cylinder. Apparently a variable species, varying in the amount and hardness of the incrustation and to some extent in the structure of the central cylinder. The extremes would doubtless be considered separate species but there are numerous intergrading forms. It appears to be closely allied to *L. tenuis* and *L. leprosa*. The irregularly dichotomous branching, the prominence of the cystocarp and the form of the cortical branchlets are constant.

Liagora hawaiiana sp. nov.

PLATE XXIV. FIG. 8, 9.

Fronde angulis acutis dichotoma ex basi parva rotundata dense decomposita, ramis multis articulis longis in diametro subaequalibus ad .8 mm. latis instructa strato calcis leve incrustata punctis multis decalcaratis minutis et in basibus articulorum singularum annulis decalcaratis interrupto, apicibus ramorum perobtusis decalcaratis; strato intimo firmo, in partibus frondis junioribus angusto, in diametro longitudine filorum corticalium minore filis cellulorum latiorum composita in partibus frondis vetustioribus latiore in diametro longitudine filorum corticalium duplo aut triplo superante; ramulis corticalibus libris dichotomis cellulis infimis cylindraceis qui fila angustissima lateralia in stratum intimum redeuntia ferunt cellulis supremis 3-5 ovalibus corymbum dichotomum subiter facientibus; frondibus dioecis, cystocarpiis plurimis ramulis dichotomis copiose involucratis, antheridiis ut in *L. leprosa,* pernumerosis.

On reef at low tide. Laie point, Koolauloa, Oahu. June 16, 1900. (J. E. T. 1005.)

The plant is large and is characterized by comparatively long internodes (1-2 cm.) and by the smooth calcareous crust which is interrupted by an uncalcified area at each node. The dichotomy of the frond is remarkably regular with no lateral proliferations and all parts of the frond are very uniform in diameter, only the basal trunks being enlarged. These characters give the plant a loosely fascicled segmented aspect. The frond, even when decalcified, is firm and almost cartilaginous.

The central cylinder consists at first of filaments about 15-20 mic. in diameter. The axis becomes much thickened in older parts of the plant by the numerous smaller filaments which originate from the lower cells of the cortical branchlets and grow along and into the central cylinder.

The proximal cells of the cortical branchlets are cylindrical, 8-11 mic. in diameter and 6-8 times as long. The same form of cell occurs above with slight decrease in diameter, the upper 3-5 cells being obovate (averaging 7x11 mic.) and forming the abrupt corymbose tips, the distal cells about one-half as large as the others. Only one or two cells occur intermediate in form between the elongated and oval cells. The lower cells bear lateral rhizoid-like filaments which form the smaller filaments of the central cylinder. In antheridial material the distal 1-2 cells of nearly all the cortical filaments bear groups of sperm-bearing filaments, the sperm cells themselves being 2-3 mic. in diameter. This appears to be a very distinct species.

Section II. **Corymbosae** sect. nov.

The following two species belong to the group represented in Agardh's revision by *L. corymbosa* alone. They stand in a somewhat intermediate position between his sub-genera. With the outward appearaance of *L. cheyneana* and the same medullary structure as is found in that species, they possess cortical branchlets resembling those of *L. leprosa*. It seems that they should be placed together in a section intermediate between Agardh's *Eu-Liagora* and *Goralia* and this section may well be termed *Corymbosae* from the typical species. As is indicated below, the first species of my collection appears to correspond most closely to Agardh's *L. corymbosa,* but I have been unable to compare my specimens with any herbarium material of that species and from the description of *L. corymbosa* it is possible that the material upon which that species

is based may correspond with either of the species in my collection or may be distinct from both of them.

Liagora corymbosa J. AG. (?) Anal. Algol. 3:104. 1896. De Toni. Syll. Alg. 4:93. 1897.

PLATE XXIV. FIG. 10.

Frond terete, on drying complanate below, somewhat terete above, dichotomous, appearing corymbose and with lateral proliferations below the corymb, apices subdivergent, the whole covered with a mealy incrustation interspersed with naked branchlets protruding beyond the crust, with the filaments of the fascicles cohering in torn series in softened material.

Waianae, Oahu. June 12, 1900. (J. E. T. 1564 C.)

Small specimens about 5 cm. high, somewhat stout, 1.5 mm. thick, dichotomously branched at somewhat long intervals and with numerous lateral proliferations. The frond has the general texture and appearance of *L. cheyneana*. The cortical branchlets have, however, the structure found in the sub-genus *Eu-Liagora*. These often arise in pretty regular order giving the frond a somewhat regular annular appearance. Below they are narrow, dichotomous at long intervals, often with somewhat open angles between the branches. The first dichotomy usually occurs at the summit of the basal cell of the filament. Above the branchlets are di- or trichotomous forming a fascicle of short spreading branchlets. The terminal cells are almost spherical, smaller than the penultimate cells, 5-8 mic. in diameter and in young branchlets are armed with setae similar to those described under *L. cheyneana*. The cortical branchlets are often 600 mic. in length. This fact, together with the spreading tips, and very slender and sparingly branched lower portions gives them a characteristic aspect. Cystocarps occur of the generic structure with a somewhat abundant involucre, resembling the vegetative cortical branchlets.

Liagora Tildenii sp. nov.

PLATE XXIV. FIG. 11, 12.

Fronde irregulariter dichotoma sed quasi subpinnatim paniculata multis cum proliferationibus brevibus ex ramis maximis exorientibus instructa, tereti, 3-5 cm. alta, ad basin 1.5 mm. lata, crusta calcis pulverulente prope ad apices ramorum tecta; strato axile in ramis junioribus perangusto, cellulis magnis per compressionem reciprocam nonnihil irregularibus instructo, in ramis vetustioribus,

longitudini ramulorum corticalium in diametro superante, filis minoribus cylindraceis multis inter cellulos majores intersertis; ramulis corticalibus inferne parce dichotomis cellulis cylindraceis longitudine quadruplum latitudinis aequantibus compositis, superne dichotome corymbosis cellulis ovatis seu rotundis moniliformibus compositis; in partibus vetustioribus frondis his ramulis dichotomis filis moniliformibus simplicibus substitutis quae ex filis medullaribus minoribus exorientur.

North of Hotel, Waianae, Oahu. May 26, 1900. (J. E. T. 861 A); Laie Point, Koolauloa, Oahu. June 18, 1900. (J. E. T. 1007); Kealea Beach, Kauai. July 25, 1900. (J. E. T. 1202.)

The frond is dichotomously decompound, but the numerous lateral proliferations give it a subpinnate aspect. The calcareous incrustation is light, mealy. The structure of the frond is that of some members of the subgenus *Goralia*. The central cylinder is very soft and in lime-free material the whole frond has a soft mucous consistency. The central cylinder consists at first of closely packed large cells with surrounding smaller filaments. At length some of the smaller filaments appear to penetrate among the larger. It is about 500 mic. in diameter in older parts of the frond, 100-200 mic. in the smaller branches. The cortical branchlets are somewhat stout, generally dichotomous at the summit of the basal cell and at intervals upward, about 300 mic. long. The lowest cell is cylindrical, emitting numerous small lateral filaments, the next cells cylindrical, about 8x40 mic., the outer cells shorter, somewhat stouter, and more contracted at the ends, with gradual transition to the outermost 3-4 cells which are short oval, forming the corymbose summit and the terminal cell almost spherical, 7-9 mic. in diameter. The cystocarps at first are plainly borne laterally near the end of a cortical filament, but they soon come to appear terminal. The involucre is composed of simple filaments or some with small abrupt terminal fascicles.

Ligaora Tildenii var. **lubrica** var. nov.

PLATE XXIV. FIG. 13.

Fronde ea typi tenuiore, lubrica, 0.5-0.75 mm. lata crusta calcis tenui pulverulente; strato axile angusto, molli; filis corticalibus inferne inaequaliter dichotomis, superne corymbos ferentibus qui super incrustationem calcis prominent.

Kauai. June 23, 1902. 18-41 fathoms. S. For. Co. R. (U. S. Fish Com. 4023 B.)

A single complete specimen most nearly resembling *Liagora Tildenii* in its branching and structure. It is much more slender than the type of this species and has the smooth texture of a *Nemalion* on account of the projection of the cortical branchlets above the calcareous stratum. The central cylinder consists primarily of filaments of large trumpet-shaped cells, each of which increases in diameter from 10-15 mic. at the base to 30-45 mic. at the upper end, where it bears the next cell of the medullary filament and also a cortical branchlet. These branchlets are shorter and much stouter below than in *L. corymbosa,* and several of the basal cells bear lateral branching filaments. The basal cells are short, irregularly cylindrical, about 10x30 mic., the median ones somewhat longer (18-10x40-50 mic.), the terminal ones broad ovate (6-8x9-10 mic.) The transition in form and size is gradual. The lowest cells bear Some of these develop directly into additional branchlets, some form auxiliary medullary filaments.

This is possibly a distinct species, but in the absence of more material, I prefer to regard it as a variety of *L. Tildenii.*

Section III. **Goralia** J. Ag.

Liagora cheyneana Harvey in Trans. Irish Acad. 22:552. 1854. De Toni. Syll. Algar. 4:94. 1897.

Frond terete, about 10 cm. long, 2 mm. in diameter at the base, tapering gradually upwards, dichotomously decompound, with a somewhat granular incrustation through which project the free peripheral filaments; central cylinder of large, closely packed cells surrounded by a layer of intertwined, small, cylindrical cells.

Kauai. June 23, 1902. 18-41 fathoms. S. For. Co. R. (U. S. Fish Com. 4023 C.)

The medullary cells bear the cortical branchlets which consist of filaments of almost cylindrical cells, the outer ones about 13x26 mic. The distal cells of the filament often bear globose antheridia consisting of short branching filaments with cells about 1.5 mic. in diameter. Other filaments bear long, filiform appendages about 2.5 mic. in diameter and 600 mic. long, somewhat clavate at the tip.

Liagora paniculata J. AG. Anal. Algol. 3:106. 1896. De Toni. Syll. Algar. 4:96. 1897.

Frond with a rugose-granulose calcareous incrustation, scarcely interrupted at the apices, terete, and densely pinnately decompound, with each branch forming a conical panicle; lower branches of the panicle often opposite, terminal apices conical, conspicuously standing out above the branches of the panicle.

Diamond Head, Oahu. April 12, 1895. (Heller 2132.)

Plants 10-12 cm. high, 1.5 mm. thick at base; axis flattened below on drying, terete above, coral red when fresh, covered with a continuous rugose granular incrustation. Central cylinder in younger parts soft, composed of large cohering filaments, in older parts larger, firmer, with many smaller secondary filaments surrounding the primary axis. The cortical branchlets as in *L. cheyneana*, sparingly branched, of short cylindrical or slightly ovoid cells about 12-15x20-25 mic.

Liagora subarticulata GRUNOW in Alg. Fidschi-Tonga und Samoa-Inseln in Journ. de Mus. Godeffroy. 6:35. 1874. De Toni. Syll. Algar. 4:97. 1897.

PLATE XXIV. FIG. 14, 15.

Frond thickish, dichotomously much branched, covered with the exception of the shortly furcate tips with a thick continuous calcareous crust, which is divided at intervals by very narrow fissures thereby dividing the frond into longer or shorter joints.

On reef at low tide.

Laie point, Koolauloa, Oahu. June 18, 1900. (J. E. T. 1007); Hanalei, Kauai. July 26, 1900. (J. E. T. 1221.)

Frond up to 7 cm. in length, 1.25-1.75 mm. wide at the base, about 1 mm. thick above the base, densely dichotomously branched, the lower angles acute, the upper obtuse, often forming dense irregularly globose masses. The tips of the branches are rounded obtuse, often shortly furcate and uncalcified. The central strand of the young branches is small, soft, consisting of rather closely packed, large, elongated cells, 30-35 mic. in diameter. From these cells arise the cortical branchlets and from the basal cells of the latter arise small cylindrical filaments which sheath, and in the older parts of the frond penetrate the central cylinder. The cortical branchlets are somewhat stout, sparingly and irregularly dichotomously or laterally branched without a definite corymbose head.

The lowest cells are large and rounded, giving rise to many of the smaller medullary filaments. The upper are cylindrical, about 10 mic. in diameter and three to four times as long, the uppermost cylindrical or somewhat oval, the terminal cells averaging about 10-15 mic. Cystocarps small, with a few simple filaments forming the involucre.

FAMILY CHAETANGIACEAE.

Galaxaura.

Key to Sections of Galaxaura.

I. Superficial parenchymatous layer without short, free assimilatory structures:

1. Parenchymatous layer not readily separable into filaments; epidermal cells flattened, bearing long, scattered, hair-like filaments.

II. *Microthoe.**

2. Parenchymatous layer loose, separable into moniliform filaments ending in a compact parenchymatous epidermis, usually without hair-like projecting filaments.

IV. *Eugalaxaura.*

II. Superficial parenchymatous layer bearing short, free projecting assimilatory structures.

1. Distinct epidermis wanting; short assimilatory filaments several-celled.

VI. *Brachycladia.*

2. Distinct epidermis present, bearing one-celled assimilatory papillae.

VII. *Vepreculae.*

Section II. **Microthoe** Dcsne J. G. Ag.

Galaxaura glabriuscula Kjellm. Om Floridé-Slägtet Galaxaura. 56. 1900.

Frond loose, patently pinnately forked, at length decompound, with solitary not crowded proliferations, subglabrous, below with small villous patches; filaments straight, elongated, up to 450 mic. in length, and 18 mic. thick; fragile, yellowish, above densely transversely rugulose; lower internodes obconical, up to 2 mm. thick

*The numbering of the sections of *Galaxaura* corresponds with that in Kjellman's monograph. In my collection there are no representatives of his sections *Rhodura, Papulifer, Heterotrichum, Laevifrons* and *Dichotomaria.* The sections as here used have the limits assigned to them by Kjellman.

and about 3 times as long, sub-distended, upper up to 10 mm. long, often shorter, obcon-ellipsoid, collapsing.

Hanalei, Kauai. July 26, 1900. (J. E. T. 1239 B.)

Some small fragments, the largest 4.5 cm. long The long peripheral filaments are very scarce except on a few stunted lower branches where they are numerous.

Galaxaura hawaiiana sp. nov.

PLATE XXIV. FIG. 16.

Fronde ad 5 cm. alta, laxe furcata, e basi crassiuscula, deinde decomposita subdivaricata proliferationibus sparsis instructa; internodis variis nunc brevibus nunc longis ad 1 mm. crassis parum seu nihil rugulosis articulis haud conspicuis; internodis infernis pilosis obconicis distentis, superis glabris elongatis cylindraceis seu fusiformibus membranaceis facile collabentibus; tela assimilatoria subparenchymata cellulis strato triplice seu quadruplici facta intimis magnis, crassis, saepe bi- seu trilobis mediis sphaericis minoribus extimis aut obconicis aut lenticularibus cohaerentibus fila periphaerica elongata in partibus frondis vetustioribus plura fragilia haec erecta stricta ad 300 mic. longa illa longiora rhizoidea saepe ramosa ferentibus.

French Frigate Shoal. May 29, 1902. 14-16 fathoms. S. Co. (U. S. Fish Com. 3968); Bird Island. August 5, 1902. 26 fathoms. Co. Corln. (U. S. Fish Com. 4147.)

The appearance of the frond is characteristic on account of the elongated, usually tapering, terminal internodes and the frequent occurrence of several very short internodes close together below which, with the divaricate branching often produces an umbellate appearance.

The parenchymatous layer is very lax, appearing in the younger internodes almost filamentous, so that these younger parts of the frond, when the elongated epidermal filaments have not yet developed, might be mistaken for parts of some *Eu-Galaxaura.* In the older parts of the frond (10 mm. or more from the growing point) the parenchyma is somewhat firmer and the development of the long epidermal filaments produces the characteristic *Microthoe* structure. In the parenchymatous area the inner cells are broad, often two or three-lobed, the unlobed cells about spherical, 30-50 mic. in diameter, the lobed up to 100 mic. wide. The intermediate cells of the parenchymatous layer are smaller, about spher-

ical, the superficial flattened obconical, with a slightly convex base, or even lenticular, 16-20 mic. in diameter. The external filaments are of two kinds, one unbranched, about 300 mic. long, composed of cells 23-30 mic. long and 15-16 mic. wide, the other longer, rhizoid-like, and often branched.

Galaxaura intricata KJELLMAN. Om Floridé-Slägtet Galaxaura. 57. 1900.

Frond growing by paired proliferations are very briefly stipitate, continuous, more or less frequently forked, at first glabrous, lightly annulately constricted, submembranaceous, collapsing, afterwards very shortly and densely hirsute, solid, distended, the lowest at length somewhat glabrous, subfarinaceous; peripheral filaments arranged in no particular order, some straight, simple. short, about 300 mic. long, others rhizoid-like, often branched, elongated; internodes barely 1 mm. thick, about 4 mm. long, not transversely plicate at the base, the upper cylindraceous-obconical, the lower cylindraceous.

Hanalei, Kauai. June 23, 1902. (U. S. Fish Com.) Diamond Head, Oahu. May 7, 1895. (Heller 2285.) (As *G. rugosa.*) (?) Kaunakakai, Molokai. Reef. April 2, 1902. (U. S. Fish Com. 3834.)

The first specimen mentioned is a form which appears in some respects intermediate between the above species and *G. cucullígera* Kjellm. The frond is small, about 4 cm. high, much branched and forming a dense mass. It has a greenish color (in material preserved in formaldehyde). The growth of the plant appears to be entirely by repeated proliferations from the summit of the previous branches. These proliferations arise in pairs, and ordinarily each proliferation forks within 1 mm. of its base so that four branches appear to rise from one point at the top of the older branch. The proliferations are forked once or twice more towards the top, the longest internodes being about 6 mm. in length, and 1 mm. in width. The youngest proliferations are glabrous, collapsing on drying and becoming faintly annulately rugose. The older proliferations are densely hirsute, especially towards the top of each segment of the frond. The oldest parts of the frond are glabrate. The cells of the innermost assimilatory layer are large, often much lobed, about 35 mic. high, 35-70 mic. wide, the cells of the middle

parenchymatous layer spherical or higher than wide, varying considerably in size, but averaging about 24 mic. in width, the superficial cells about 18 mic. in diameter, almost spherical, or higher than wide. The elongated peripheral filaments are 17-18 mic. in diameter and seldom exceed 200 mic. in length. Rhizoid-like filaments occur but are rare. The joints at the base of the proliferations are very short. The peripheral filaments at the base of one of these joints are elongated, cylindrical filaments resembling those of the internode. Above occur shorter filaments, often branched, with clavate ends, the terminal cell about 30 mic. in diameter and then yet shorter filaments with the two upper cells tumid, from which the transition is rapid to the ordinary sub-parenchymatous peripheral layer.

Heller's specimen is a somewhat larger plant than the above, about 5 cm. high, and with internodes up to 6 mm. long and 1.5 mm. wide. In mode of branching and structure it agrees with the above.

No. 3834 U. S. Fish Com. agrees with the above in structure, but differs in color, being whitish, and is less regularly branched, many of the proliferations being striated and the whole specimen having the aspect of a plant which has grown under unfavorable conditions.

Galaxaura cuculligera KJELLM. (?) Om Floridé-Slägtet Galaxaura. 58. 1900.

Frond umbellate, with proliferations which are very short, stipitate, more or less densely forked, at first glabrous, smooth or densely rugulose, membranaceous, collapsing, with the lowest internode cucullate, afterwards densely villous, solid, distended, heavily impregnated with lime, subcylindraceous, with almost inconspicuous joints; elongated peripheral filaments persistent, not arranged in any conspicuous order, often branched, the branches either similar, strict, sub-attentuated, short, or one branch strict, the other rhizoid-like, much elongated.

Waianae, Oahu. May 22, 1900. (J. E. T. 821 B.)

A single plant agreeing with the description of this species except that the peripheral filaments are strict, simple. Often, however, two are borne side by side on the same subepidermal cell, giving somewhat the appearance of a forked filament.

Section IV. Eugalaxaura (Dcsne) Kjellman.

Galaxaura fragilis LAMK. et auct. in Kjellman. Om Floridé-Slägtet. Galaxaura. 60. 1900. Tilden. American Algae. Cent. V. no. 415. 1901. (*G. adriatica.*)

Frond corymbose, very smooth, fragile, almost inconspicuously annulately rugose, pale, with white apices, about equally thick throughout, equally dichotomous, at length decompound with proliferations growing out from the summits of broken branches, axils open, internodes obconical or cylindraceous, obconical, with length four times the diameter, below 1.7 mm. thick; assimilatory filaments not joined when the lime is dissolved out, composed of cells with thin walls, the inner round or with a width greater than the height, commonly 36-42 mic. wide, the terminal subequal, semiglobose, 18-20 mic. wide. Attached to rocks on sandy beach.

Waianae, Oahu. May 22, 1900. (J. E. T. 827.)

Kealia beach, Kauai. July 25, 1900. (J. E. T. 1178 A.)

The cortical cells are somewhat smaller than above. The inner cells average about 30 mic., the outer about 18 mic. According to Kjellman (in letter) this material, if not identical with the above species, is very closely allied to it.

Det. by Kjellman.

Galaxaura schimperi DCSNE. Sur les Corallines. 116. 1842. Kjellman. Om Floridé-Slägtet. Galaxaura. 61. 1900.

Frond loosely corymbose or almost semi-globose, very smooth, somewhat firm, above densely annulately elevated rugose, yellowish, thickened towards the apex, loosely equally furcate and decompound with proliferations from the apices, and sometimes from the geniculi; axils wide; internodes distended, elongated obconical. the lower 2 mm. wide and 1.5-3 times as long, the upper more elongated, up to six times the diameter; filaments of the assimilatory tract not connected when the lime is removed, consisting of cells with thin walls, the interior obovoid or ovoid, their height exceeding their width, scarcely exceeding 30 mic. in diameter, the uppermost often obconical, of various size, 8-12 mic. wide.

Hanalei, Kauai. July 25, 1900. (J. E. T. 1239.)

Section VI. **Brachycladia** Sonder. Linnaea. 514. 1853.

Galaxaura arborea KJELLM. Om Floridé-Slägtet. Galaxaura. 72. 1900.

Stalk very stout, elongated, attenuate towards the apex, above fasciculately or subverticillately branched; leaves shortly dilated, widely obovate, several times pinnate furcate, thickish, whitish, with internodes 2-3 mm. wide, barely more than 5 mm. long, with assimilatory filaments having almost always a unicellular pedicel; terminal cells commonly cylindraceous-elliptical, 40-48 mic. long, 24-36 mic. wide.

Laysan Island. May 21, 1902. 16 fathoms. S. Co. (U. S. Fish Com. 3962.) Bird Island. June 3, 1902. 32-46 fathoms. S. For. R. (U. S. Fish Com. 3978.) Bird Island. August 8, 1902. 40-56 fathoms. Co. S. P. Sh. (U. S. Fish Com. 4164.)

In some plants in this material the stalk is comparatively short and branched almost at the base, while in other plants it is as long as Kjellman's description indicates. This difference appears to be entirely a matter of individual variation.

Galaxaura acuminata KJELLMAN in Mss.

PLATE XXIV. FIG. 17-19.

Fronde ad 8 cm. alta paniculata e caudice brevissimo prolificationibus plurimis iteratim laxe furcatis teretibus aut superne subcomplanatis, inferne subglabra sed filis rectis paucissimis sparsis aut subverticillatim dispositis instructa, superne fere glabra transversim striata; tela assimilatoria filis curtis plerumque cellulis ternis compositis cellula proxima singula ultimas binas ferente ellipsoideas saepe breviter apiculatas 30-35 mic. longas, 15-25 mic. crassas (rare majores) chromatophoro hemisphaerico valido praeditas instructa.

Waianae, Oahu. May 22, 1900. (J. E. T. 821.) Type specimen.

On sides of shaded rocks at half tide. Oahu. (J. E. T. 1084.)

Specimens from the type collection were determined by Kjellman in 1902 as being a new species to which, in a letter, he assigned the name *Galaxaura acuminata*. This species has, however, never been published. The description given above is from material of the same collection now in the Botanical Department of the University of Minnesota. The stalk of the frond is short and bears many proliferations, each of which is many times dichoto-

mous. The internodes are 4-10 mm. in length (usually about 6 mm.), .75-1.5 mm. wide and .5-1.25 mm. thick, each internode slightly wider at the distal than at the proximal end. The lower internodes are terete, slightly rugose and furnished with a very few long hairs which in some specimens are scattered and in others are verticillately grouped at the lower nodes. The upper internodes vary to a considerable degree in the several plants. In some they are quite terete, in others flattened and about twice as wide as they are thick. The upper internodes are entirely glabrous and marked with transverse striations.

The medullary portion of the frond is composed of intertwined filaments, 7-12 mic. in diameter. The parenchymatous layer consists of about three layers of elliptical, spherical or slightly angled cells, the innermost about 65 high by 40 wide, the outer ones 20-30 mic. high, 45-55 mic. wide. The assimilatory filaments are borne upon the middle layer of the parenchymatous cells, their stalks intervening between the cells of the outer layer. Two or three of these filaments may be borne upon a single cell of the parenchymatous layer. The filaments are typically three-celled. The basal cell is about 17 mic. high by 7-10 mic. wide, forked at the summit. It commonly bears two distal cells. These are narrowly or widely elliptical or ovate, rounded at the distal end or shortly mucronate, and have hemispherical chromatophores which fill about the distal one-third of the cells. Among these filaments are the few long hairs mentioned above, which are straight, unbranched, about 700 mic. long and 10 mic. thick. They are very rare in the upper parts of the frond and not abundant anywhere.

Galaxaura mauiana sp. nov.

PLATE XXIV. FIG. 20.

Fronde at 6 cm. alta e caudice brevissimo hirsuto prolificationibus plurimis iteratim furcatis inferne teretibus superne subcomplanatis aut paene teretibus, inferne hirsuta filis rectis plerumque simplicibus aut fere glabra, superne subglabra transversim striata; tela assimilatoria filis curtis plerumque cellulis ternis vel quarternis compositis cellula proxima singula ultimas aut binas aut ternas ferente ovates rare apiculatas 35-46 mic. longas, 20-27 mic. crassas, chromatophoro conspicuo complanato praeditas qui partem quartam cellulae supremam implet instructa.

Napili Harbor, Maui. April 16, 1902. (U. S. Fish Com. 3881 A.)

This form very closely resembles *Galaxaura acuminata* and very possibly is a variety of that species. In external appearance it differs from *G. acuminata* only in its greater pubescence, especially in the region of the caudex. This is in some plants markedly hirsute and in all cases the long hairs are much more abundant than in *G. acuminata.* Under the microscope it can be distinguished from that species by the structure of the parenchymatous layer and by the terminal cells of the short assimilatory filaments. The cells of the cortical layer are more firmly joined into a parenchyma than in *G. acuminata.* The inner cells of the cortical layer are much broader than in that species, 50-60 mic. high by 70-90 mic. wide. The cells of the outer layers are much as in that species, about 25 mic. high by 50 mic. wide.

The assimilatory layer is borne as in *G. acuminata* and has the same structure as in that species. The basal cell averages 20 mic. high by 12-15 mic. wide. The distal cells vary considerably in size and shape, the most common form being ovate or somewhat pear-shaped, with the broadest part below. As in *G. acuminata* they are usually rounded at the summit, but sometimes apiculate. The chromatophore is very conspicuous and is crowded into the distal one-fourth or even one-fifth of the cells, the remaining portion being quite hyaline.

Section VII. **Vepreculae** Kjellm.

Galaxaura hystrix Kjellm. (?) Om Floridé-Slägtet. Galaxaura. 79. 1900.

Arborescent; frond consisting of an elongated, terete, spongy trunk and flattened, forked leaves; each cell of the superficial layer bearing a single clavate, briefly apiculate papilla, 25-30 mic. long, above about 17 mic. in diameter.

Bird Island. August 8, 1902. 40-56 fathoms. Co. S. P. Sh. (U. S. Fish Com. 4164.)

A single somewhat fragmentary specimen which may very probably belong to a new species allied to the above. The general aspect of the frond agrees closely with the above. It is arborescent, about 6 cm. high, with a proliferating trunk about 1.5 mm. in diam-

eter, which rises from an enlarged base. The branches of the trunk bear thin, forked leaves. The segments of the leaves are about .5 mm. thick, 2 mm. wide, 4-12 mm. long, cuneate or linear-cuneate. The "leaves" are distinctly thickened along the margins and are very faintly transversely zonate towards their outer ends. The trunk is solid cylindrical, slightly limy throughout, its peripheral layer consisting of short free filaments with their outer cells swollen, about 30 mic. in diameter. The leaf consists within of loosely interwoven filaments. The assimilatory layer consists of thin layers of cells. The innermost layer consists of large cells broader than high. The middle layer is made up of somewhat larger cells, often lobed, and when not lobed higher than broad. The outermost layer consists of small flattened cells about 25 mic. in diameter, those on the margin of the leaf bearing each a single clavate, cylindrical, apiculate papilla 40-45 mic. long, about 14 mic. wide above.

The greater size of the cortical papillae, their distribution, and the absence of elongated cortical filaments in the region of the stipe, appear to distinguish it from the species as described by Kjellman.

Galaxaura infirma KJELLM. Om Floridé-Slägtet. Galaxaura. 81. 1900.

Frutescent; frond loose, forked, with the internodes often evidently contracted at the base, scarcely more than 1.5 mm. wide, with close set superficial papillae, subclavate cylindrical, rounded or often acutish at the apex, not rarely short-mucronate, 25-30 mic. long, about 18 mic. wide.

On rocks at half tide.

Waianae, Oahu. May 22, 1900. (J. E. T. 820.)

Det. by Kjellm.

Kealia beach, Kauai. July 25, 1900. (J. E. T. 1178.)

Galaxaura sp.

PLATE XXIV. FIG. 21.

A form apparently intermediate between *G. infirma* and *G. veprecula* Kjellm. It is more loosely branched than the above and has thinner and wider branches with the internodes distinctly contracted and jointed at the base. The outer cells of the assimilatory area are subhemispherical, not so much flattened as in *G. infirma*,

bearing papillae which are clavate, rounded at the apex, or more frequently acutish and shortly mucronate, 32-40x14 mic.

Napili harbor, Maui. April 16, 1902. Reef. (U. S. Fish Com. 3881 B.)

EXPLANATION OF PLATE.

PLATE XXIV.

All drawings are magnified 150 times, except where otherwise stated. The drawings of Liagora consist of a cell of one of the central filaments and an attached cortical branchlet, except where otherwise noted. The drawings of Galaxaura show a group of cortical cells.

1. Liagora pulverulenta Ag.
2. Liagora tenuis J. Ag.
3. Liagora maxima sp. nov.
4. Liagora maxima. Cortical filaments from proximal part of a branch.
5. Liagora maxima. Antheridial cells, X 250.
6. Liagora intricata sp. nov.
7. Liagora sub-paniculata sp. nov.
8. Liagora hawaiiana sp. nov.
9. Liagora hawaiiana. Antheridial cells, X 250.
10. Liagora corymbosa J. Ag.

13\. Liagora Tildenii var. lubrica var. nov.

12\. Liagora Tildenii. Cystocarp.

11\. Liagora Tildenii sp. nov.

14\. Liagora subarticulata Grunow.

15\. Liagora subarticulata. Antheridial cells, X 250.

16\. Galaxaura hawaiiana sp. nov.

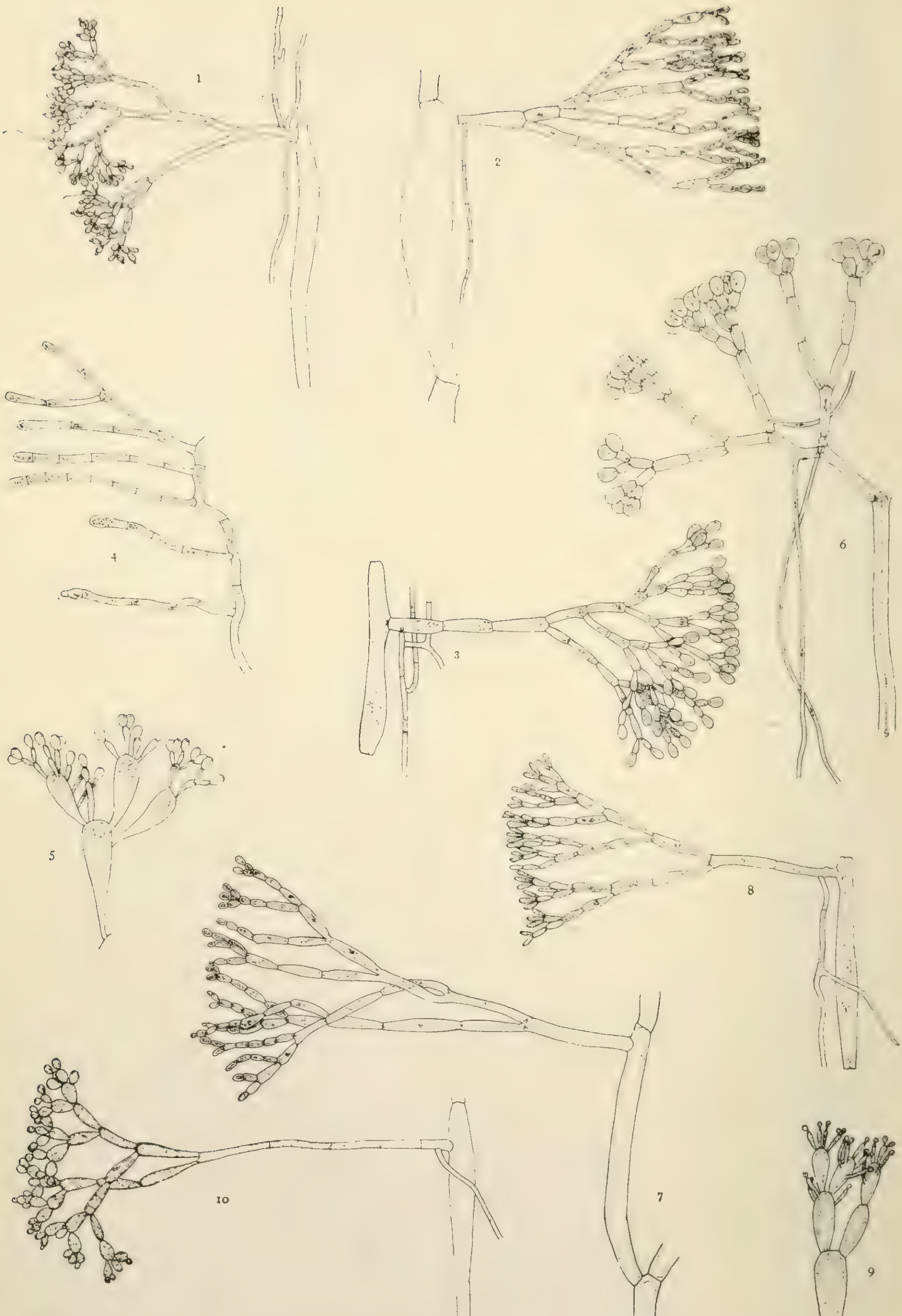
17\. Galaxaura acuminata Kjellman.

18\. Galaxaura acuminata Kjellman.

19\. Galaxaura acuminata Kjellman.

20\. Galaxaura mauiana sp. nov.

21\. Galaxaura (Section Vepreculae) sp.



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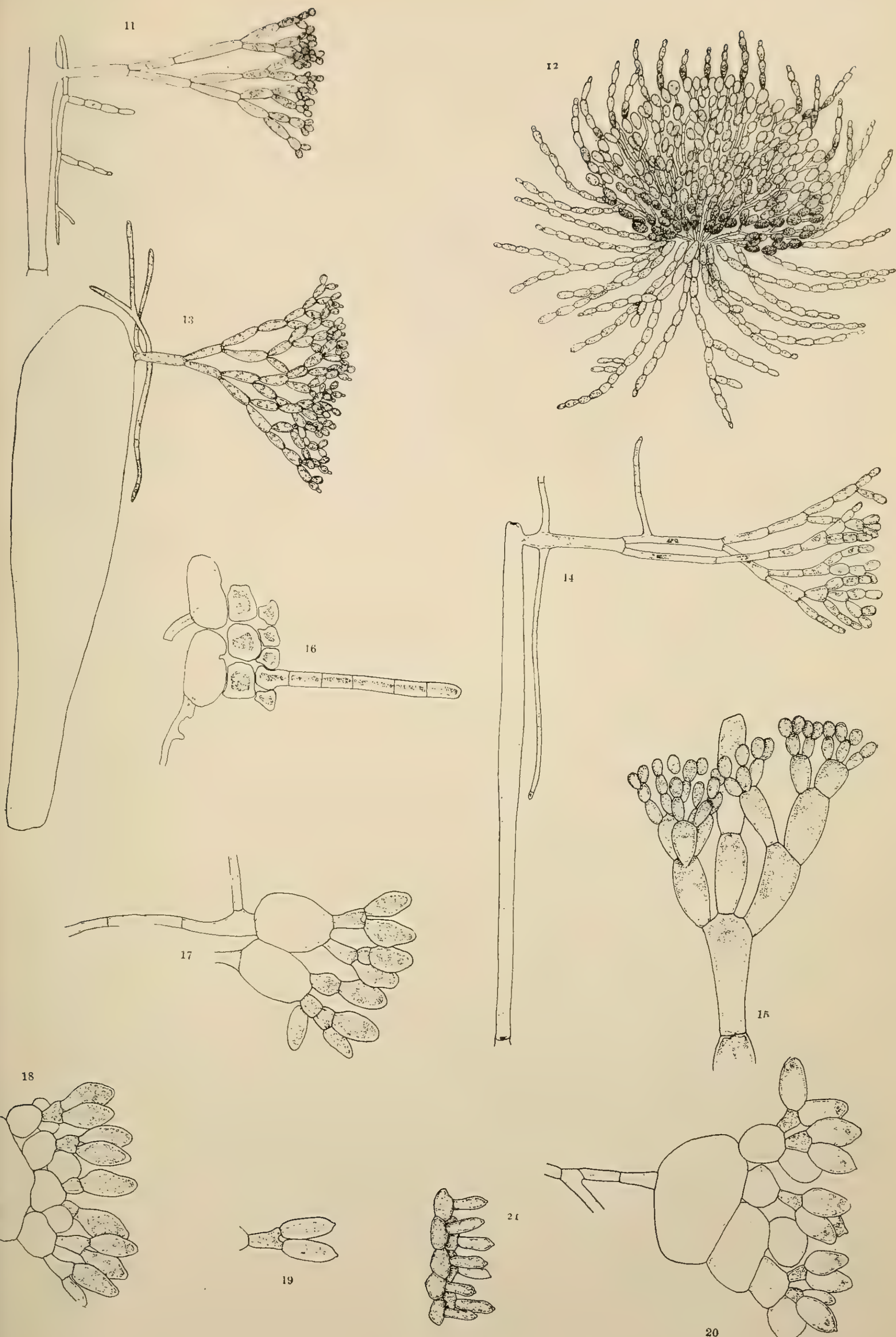
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NOVA FUNGORUM COLORADENSIUM GENERA.*

FREDERIC E. CLEMENTS.

Sphaeriaceae.

Comoclathris.

Perithecia plerumque gregaria vel copiosa, tecta vel mox epidermide evanida superficialia, membranacea vel submembranacea, globosa, vix aut non papillata, nigra, setosa. Asci clavati vel oblongi, typice octo-spori. Paraphyses filiformes vel clavulatae. Sporae ellipticae ovoideaeque, applanatae, muriformes, aureae vel brunneae. Nomen propter perithecium pilosum clathrosporumque; κόμη, hair; κλάθρις, lattice. Typus *C. lanata!* Est *Clathrospora pilosa* seu *Pocosphaeria* sporis applanatis.

Comoclathris lanata.

PLATE XXV. FIG. 1.

Peritheciis plerumque gregariis, tectis, deinde epidermide evanida superficialibus, submembranaceis, depresso-globosis, ostiolatis, vix vel non papillatis, setis simplicibus rigidis multiseptatis fumosis versus apicem pallidioribus, raro distincte asperulatis, 150-250 × 4-5 mic. in epidermide radiatim fixis dense obsitis, nigris, 250-450 mic. diam.; ascis octosporis, late clavulatis vel oblongis, breviter stipitatis, 100-125×20-25 mic.; paraphysibus paucis, filiformibus superne clavulatis; sporis irregulariter distichis, applanatis, ellipsoideis vel ovoideis, 5-septatis, 4 cellulis internis longitudinaliter 1-divisis, vix vel non constrictis, 24-27 × 15 mic. acie 6-7 mic. Nomen propter perithecium lanatum.

In caulibus vetustis *Leptotaeniae multifidae Picea engelmannii*-hylio, Silverton, 2800 m. Julii, 1907. (Crypt. Form. Colo. 444.)

Comoclathris ipomoeae.

Peritheciis gregariis vel copiosis in areis nigricatis indeterminatisque, diu vel persistenter tectis, membranaceis, globosis dein cupulato-collapsis, inferne setis brunneis simplicibus brevibus vix septatis 100-120×4-6 mic. crebre circumdatis, superne calvis, magnis, 400-500 mic. diam.; ascis octosporis, clavulato-cylindricis, stipitatis, 75-100×15 mic.; paraphysibus numerosis, filiformibus; sporis oblique monostichis vel distichis, applanatis, oblongo-ovoideis, 4-sep-

* Cfr. Clements, "Genera of Fungi," 173. 1909.

tatis, 2 cellulis internis latioribus longitudinaliter 1-divisis, ad septa constrictulis, 20-24×9-10 mic. acie 6-7 mic. Nomen propter plantam altricem. In caulibus vetustis *Ipomoeae leptophyllae Bouteloua-Andropogon-psilio,* Wray 1100 m., Augusti, 1907, (sub nomine *Pyrenophora ipomoeae* (450) Cryptogamis Formationum Coloradensium edita).

Pezoloma.

Apothecia superficialia, sessilia, plerumque ceracea, cupulata vel scutellata, dentibus triangularibus ciliato-marginata, excipulum prosenchymaticum, achroum. Asci octospori, anguste cylindracei. Paraphyses simplices, filiformes. Sporae oblongae, continuae hyalinae. Nomen propter cupulam dentibus ciliatam; πέζις cup, λόμα fringe. Typus *P. griseum!* Est *Cyathicula sessilis.*

Pezoloma griseum.

PLATE XXV. FIG. 2.

Apotheciis superficialibus, sessilibus, plerumque sparsis, ceraceis vel coriaceo-ceraceis, cupulatis vel scutellatis, margine eximie dentibus gracilibus trigonis ciliata, dentibus acuminatis denticulatis hyalinis vel griseis, 150-200 mic. long, 10-12 mic. ad basim, ½-2 mm. lat., hymenio griseo, paraphysibus simplicibus filiformibus hyalinis, 120×2 mic.; excipulo prosenchymatico griseolo; ascis octosporis, anguste cylindraceis. iodo non tinctis. 110-120×9-10 mic.; sporis oblongis vel fusoideis, continuis hyalinis distichis minute polari-guttulatis, 15-18×3-4 mic. Nomen propter apothecii colorem.

Ad et inter radiculas udas *Betulae occidentalis Picea-Pseudotsuga-hylio,* Minnehaha 2700 m., Julii, 1906. (Crypt. Form. Colo. 292.)

Phalothrix.

Apothecia superficialia, sessilia vel subsessilia, ceracea vel coriaceo-ceracea, scutellata, pilis eseptatis rigidis nitidis obsita, excipulo prosenchymatico. Asci octospori, clavulati. Paraphyses filiformes, superne clavulatae. Sporae oblongae vel fusoideae, continuae hyalinae, raro 1-septatae. Nomen propter pilos nitidos; φάλος shining, θρίξ thread. Typus *P. hyalotricha* (Rehm)! Est *Dasyscypha* pilis unicellularibus nitidis.

Leucopezis.

Apothecia subsuperficialia, sessilia vel substipitata, carnoso-ceracea, cupulata, albo-pilosa sed non ciliato-marginata; hypothecium crassum. Asci octospori, cylindracei, iodo non tincti. Paraphyses simplices clavulatae. Sporae ellipsoideae, continuae, hyalinae, leves. Nomen propter cupulam albo-pilosam, λευκός white, πέζις cup. Typus *L. excipulata!*

Leucopezis excipulata.

PLATE XXV. FIG. 3.

Apotheciis superficialibus vel interdum insculptis, subsessilibus, solitariis vel gregariis, carnoso-ceraceis, cupulatis, rarius scutellatis, pilosis, margine crenulata, interdum hirsuta sed haud ciliata, hymenio aurantiaco, extus concoloribus, inferne pallidioribus, 1-5 mm. lat.; paraphysibus simplicibus clavatis, septatis, undique granulis minutis aurantiacis asperatis 4 mic. lat., clava longe, dilute aurantiaca, 6-7 mic. lat.; hypothecio crasso, homogeneo, filamentis crebro rotundato-inflatis composito, 300-400 mic. cr.; excipulo distincto, elevato, pilis parallelis septatis dilutissime aurantiacis 120-150×6 mic. obsito, inferne pilis hyalinis compositis interdum ramosis; ascis octosporis cylindraceis, stipitatis, operculatis, iodo non tinctis, sed clavis paraphysium et pilis iodo virescentibus, 300×25 mic.; sporis monostichis, ellipticis, hyalinis, levibus, gutta 10 mic. lat. praeditis, 20-24×15-16 mic. Nomen propter excipulum distincte elevatum.

Ad terram muscosam *Salix-Betula*-helodrio, Mountain View, Pike's Peak 2800 m., Julii, 1905. (Crypt. Form. Colo. 117.)

Sirodothis.

Pycnidia erumpentia, aggregata, sed distincta et non vel paulo stromatica ad basim, primitus clausa dein perforata, vix papillata, carbonacea, glabra, globoidea, nigra. Basidia filiformia plerumque ramosa fasciculata. Conidia oblonga continua hyalina pleurogena vel acrogena, ramose concatenata. Nomen propter pycnidium dothiorum conidiis catenatis. Typus *S. populi!* Est *Peckia* aggregata; *Dothiorella* conidiis catenatis.

Sirodothis populi.

PLATE XXV. FIG. 4.

Pycnidiis erumpentibus 2-8-aggregatis, ad basim paulo stromaticis, clausis dein perforatis, carbonaceis, glabris, globoideis, 200-

350 mic. diam., gregibus ½-1mm. diam.; basidiis filiformibus congestis, septatis, ad basim ramosis, minute torulosis, catenis plerumque singulis, ad septa, et unilateralibus saepius binis ad apices, 35-50 ×3 mic.; conidiis oblongis hyalinis, 2-20 in catenis saepe dichotome ramosis, 3×1 mic. Nomen propter plantam altricem. In ramulis vetustis *Populi tremuloidis Populus tremuloides*-hylio, Long's Peak Inn 2700 m., Augusti, 1907. (Crypt. Form. Colo. 478.)

Sirocyphis.

Pycnidia superficiatia, discreta, primitus globoidea deinde late aperta vel cupulata, laeticoloria vel alba, mollia, membraneo-ceracea vel carnosa, pilis rigidis dense obsita. Basidia simplicia filiformia. Conidia oblonga vel bacillaria continua hyalina longe-catenata in catenis simplicibus. Nomen propter pycnidium cupulatum conidiis catenatis. Est *Chaetozythia* vel *Cyphina* conidiis catenatis seu *Sirozythia pilosa*. Typus *S. nivea!*

Sirocyphis nivea.

PLATE XXV. FIG. 5.

Pycnidiis superficialibus subgregariis, globosis vel suboblongis, oreolato apertis vel subcupulatis, siccitate clausis, albis, mollibus, ceraceis, exciplo subparenchymatico, extus pilis hyalinis rigidis simplicibus fere solidis eseptatis plerumque rectis attenuato-acutis 100-150×6 mic. dense obsitis, 250-400 mic. lat.; basidiis simplicibus filiformibus 20×1 mic.; conidiis oblongis vel bacillaribus, continuis hyalinis utrinque truncatis vel obtusis, eguttulatis, rectis in catenis simplicibus brevibus digestis 5-6×1 mic. Nomen propter colerem niveum.

Ad caulos vetustos *Pedicularis racem sae Picea*-hylio, Long's Peak 3000 m., Augusti, 1907. (Crypt. Form. Colo. 497.)

EXPLANATION OF PLATE.

PLATE XXV.

1. Comoclathris lanata: a, perithecia ×30; b, ascus and paraphyses ×400; c. hair ×400; d, spore, side view ×400.
2. Pezoloma griseum: a, cup ×25; b, ascus and paraphyses ×400; c, tooth ×400.
3. Leucopezis excipulata: a, cup ×4; b, ascus and paraphyses ×400; c, hair ×400.
4. Sirodothis populi: a, pycnidia ×30; b, basidia and conidia ×400.
5. Sirocyphis nivea: a, pycnidia ×30; b, basidia and conidia ×400; c. hair ×400.

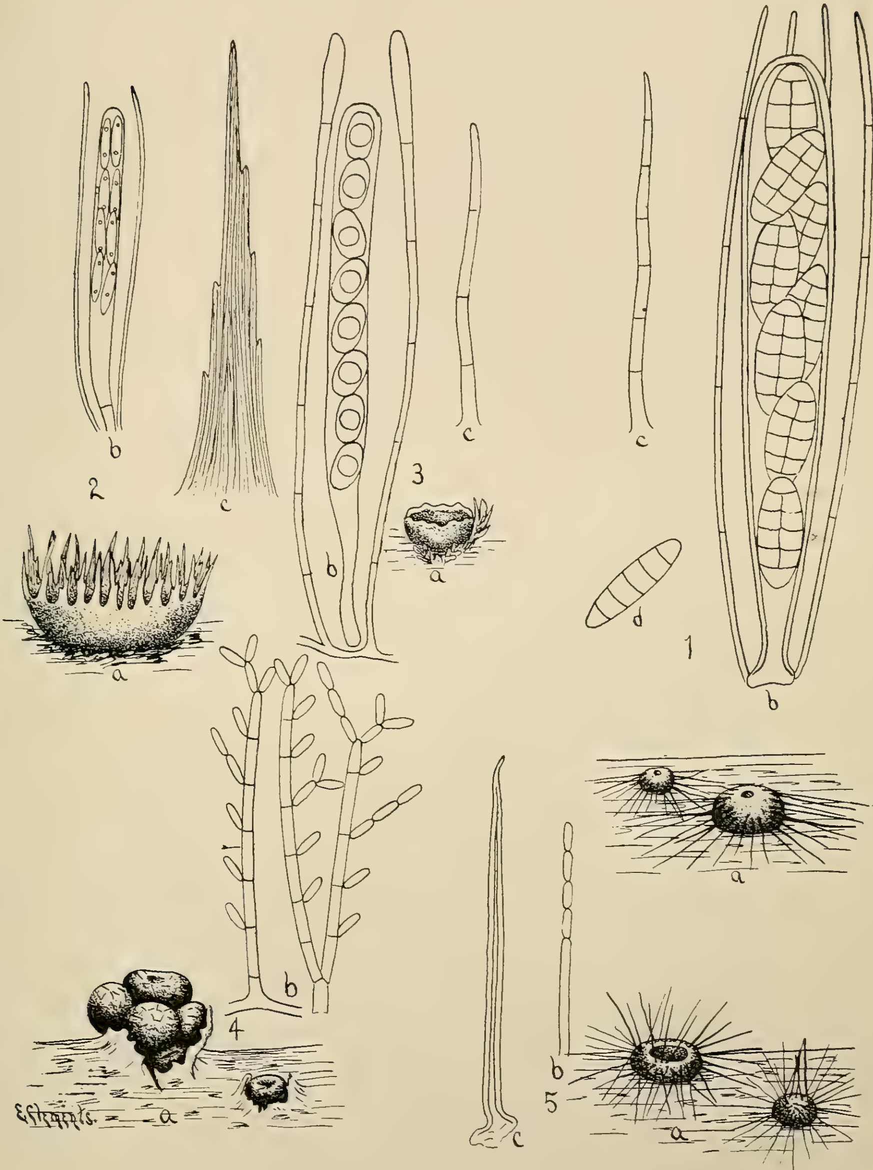


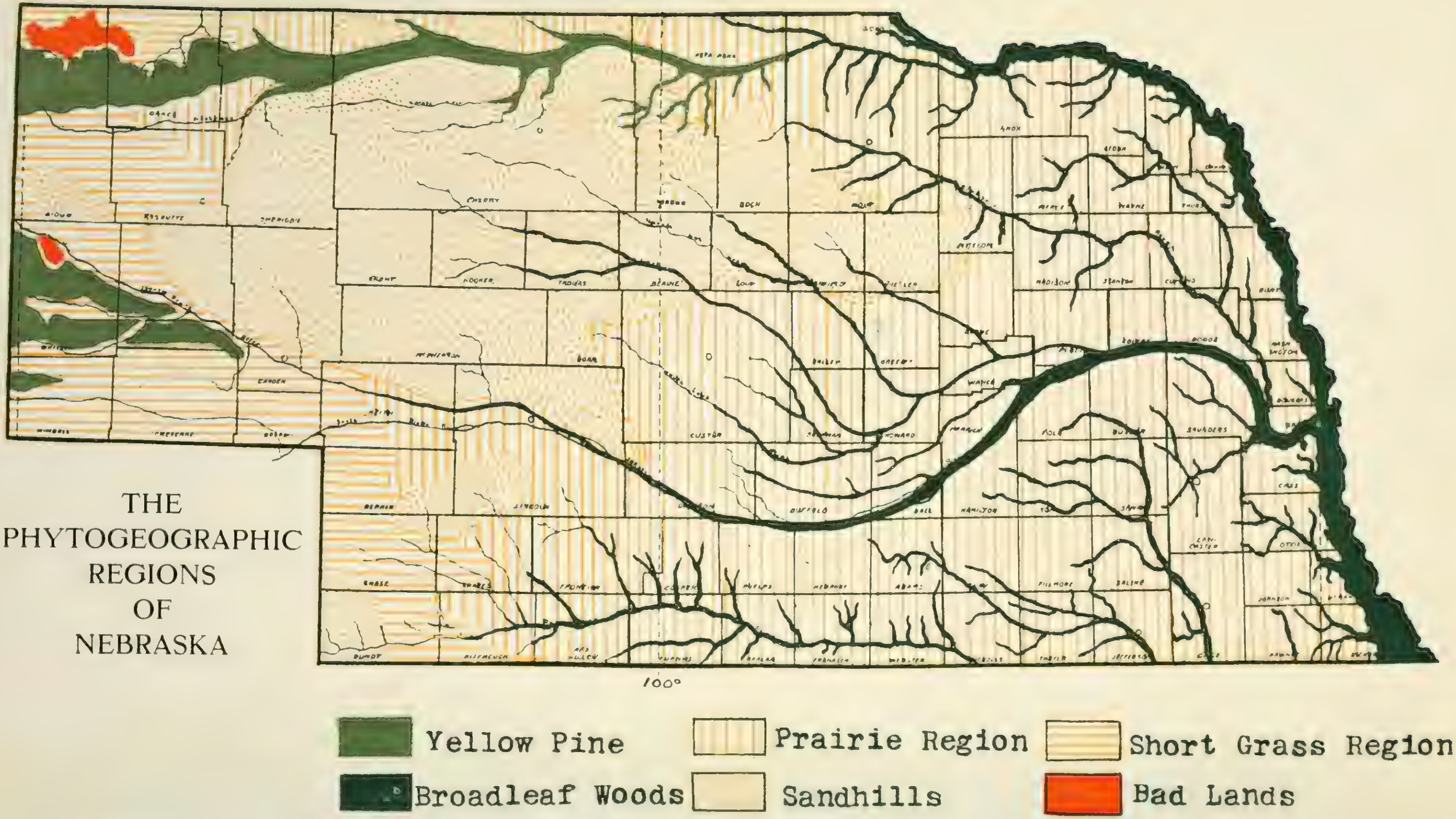
PLATE XXV

Geological and Natural History Survey of Minnesota
Frederic E. Clements, *State Botanist*

Minnesota Botanical Studies

PART III
VOLUME IV

University of Minnesota
Minneapolis
March 15, 1914



Broadleaf species occur in the canyons of the yellow pine region but it is impractical to show this fact on a map so small. The prairie-grass and short-grass regions also overlap much more than is shown on the above map.

GEOLOGICAL AND NATURAL HISTORY SURVEY OF MINNESOTA
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CONTENTS

Stops for observation and discussion were made at strategic points every few miles. From the first point, elevation 590 feet, the subaerial valley forms below the Prospect terrace were noted. Here, as is generally true in any one view, nothing more than one older, outer, and higher, one younger, inner, and lower valley slope is demonstrable; yet a broader study of the region suggests that the valleys had been eroded here with respect to older base-levels of about 620 and 520 feet, and several younger and lower base-levels. It emphasized the need in physiographic study of an analytical investigation of a region from the map as a necessary accompaniment of local field observation.

The next stop was at an elevation of 900 feet on the top of a remnant of the Prospect terrace. Here again, as in most cases, nothing conclusive is shown by observation at one point in regard to the mode of origin of the Prospect terrace or its relation to the higher levels. A broader study suggests, however, that it was made by a marine planation of moderate amount resulting from a submergence following a long period of subaerial erosion.

The three higher terraces, on the other hand, as shown on the route through Morris, Litchfield, and West Goshen, show very definitely plains cut nearly horizontally, but at successively higher levels. From the viewpoint of each lower plain, the front of the next higher terrace is seen to trend as a dissected and sloping wall across the landscape. The surface of each higher terrace has suffered also to a greater extent than those lower from subsequent subaerial denudation.

The consequences following from this interpretation of the Piedmont plateau are most important, as it changes the conception of its mode of origin and of the Tertiary history of the Atlantic slopes. It gives a suggestion of the geological rapidity of completion of an erosion cycle in a region near the sea and of a sequence of diastrophic rhythms there recorded. A similar control of the topography of the seaward slopes should be applied as a working hypothesis as a competitor of the older explanation for other portions of the Atlantic shores.

THE SAND HILLS OF NEBRASKA[1]

About 20,000 square miles in central and western Nebraska, with smaller areas in neighboring states (mostly between 2000 and 3000 feet above sea-level) are characterized by sand-hills unlike those of any other part of the world. Professor Pool has now written a comprehensive account of this region. His monograph discusses the history of exploration of the area, its location and extent, geology and soils, topography and drainage, climate, effects of fire, soil moisture and texture, and plant ''formations'' and associations (this topic covering nearly 100 pages), and closes with a bibliography and thirty excellent half-tones.

The region is underlaid by Tertiary sandstones, the weathering of which has produced a soil consisting almost wholly of quartz sand on the uplands, with

[1] A Study of the Vegetation of the Sand-hills of Nebraska. By Raymond J. Pool. Map, ills. *Geol. & Nat. Hist. Surv. of Minnesota Botanical Studies*, Vol. 4, Part 3, pp. 189–312. Univ. of Minnesota, Minneapolis, 1914. 9½ x 6½.

some admixture of silt in the hollows. No chemical analyses of the soils are given, but determinations of humus and nitrogen for a few samples are quoted from another paper.

The topography is irregularly undulating, with a local relief of 100 feet or more in many places, and characterized by innumerable ''choppy'' hills and basins, some of the latter occupied by lakes, ponds, or marshes. Small streams are scarce, but there are a few rivers which have cut canyon-like valleys in the sandstone. A very characteristic topographic feature is the ''blow-out,'' formed wherever breaks in the carpet of vegetation caused by fire or over-grazing allow the wind to scoop out hollows in the sand, which may become 100 feet deep and 600 feet wide before the vegetation regains a foothold. Outside of the blow-outs there is no noticeable movement of the sand.

The region is semi-arid, the average annual precipitation being about twenty inches. The author says nothing of the seasonal distribution of rainfall, but Plate 2 in *U. S. Geol. Survey Water Supply Paper 234*, 1909, shows that this sand-hill country is in or near the only part of the United States which has over 80 per cent. of its rainfall in the six months April–September; from which it is natural to conclude that there is some correlation between the extremely sandy soil and the excess of summer rain, as has been pointed out by the reviewer for some parts of the southeastern coastal plain.

The country is essentially treeless, except along streams. The vegetation is divided into about two dozen ''associations,'' and the plants of each are listed, mostly in alphabetical order, instead of in order of abundance, which would have been much more significant. The most extensive type of vegetation is the ''bunch-grass association,'' and the most abundant plant in it is the common grass *Andropogon scoparius* (called broom-sedge in the East). The vegetative covering, unlike that of dunes and deserts, is in most places dense enough for fire to run through it at intervals; and this monograph is one of the very few ecological papers that recognizes the importance of fire as an environmental factor, instead of treating it as a mere accident and dismissing it in a few words. The author says that many of the fires are started by lightning, a fact which some ecologists who have studied prairie vegetation farther east seem loath to admit.

Although little is said about the economic features, it is evident from the illustrations that the area is very sparsely settled. (It had about two inhabitants to the square mile in 1910, and sod-houses are the most characteristic type of architecture.)

The bibliography, exclusive of cross-references, contains seventy-three titles, some relating to the area studied and some merely of general interest. It would have been appropriate to add the ''Reconnoissance Survey of Western Nebraska,'' by T. D. Rice and party, in *Field Operations of the U. S. Bureau of Soils for 1911* (pp. 1875-1989, Plate 17), the separates of which were issued in June, 1913.

ROLAND M. HARPER.

1. A STUDY OF THE VEGETATION OF THE SANDHILLS OF NEBRASKA

Raymond J. Pool

INTRODUCTION

When Professor Bessey began his work at the University of Nebraska in 1884 he found a state and a flora that were practically unknown to botanists. Except for the scattering notes of early explorers and trappers and a few meagre collections, very little indeed was available to indicate even in a most general way the now well-known diversity of the plant life of this state. Soon there were a number of young men attracted to Professor Bessey's department in the university who became greatly interested in the flora and the general habitat relations of the flora of Nebraska. As a consequence of this early spirit, which assumed a strong ecological trend, the Botanical Survey was organized and has been continued for twenty-seven years until there are few states in America whose vegetational characteristics are better known than those of Nebraska. During these earlier studies the sandhill region was naturally the scene of a number of botanical expeditions which resulted in the collection of a considerable mass of data concerning this area which is in many respects unique among our natural phytogeographic regions.

The first careful botanical work in the sandhills was done by Webber during the summer of 1889. In the report (76) of this expedition we have the first authentic account of floral conditions in the sandhills. The same report includes also the "Catalogue of Plants," which served for so many years as a guide to the collection and field study of the native plants of Nebraska. Notes on the collections, a list of species from the central sandhills, and some comments upon preëxistent forests of the region constitute additional valuable contributions to the knowledge of the biology of the region

under study. During this same year Webber published a list (74) of the freshwater algae of the plains. A brief paper (73) on the flora of central Nebraska published by this author in the American Naturalist for 1889 includes practically the same preliminary sketch as was indicated under the first reference. Bates (4) in 1892 published a paper on the grasses of northwest Nebraska which includes notes on a number of sandhill species. The vegetation of Box Butte and Cheyenne counties was studied by Smith (62). In this paper we have a contribution to the knowledge of the grass flora of the western border of the sandhills. Bessey in a series of papers touched upon a number of the characteristics of the vegetation of this region and in these papers (7, 10, 11, 12, 13, 16) we find numerous valuable lists of species, and suggestions as to the origin (14, 15) of the flora of the state. Bessey is of the opinion (13) that the sandhill region was at one time more or less forested and he recommended (12, 13) that experiments in reforestation should be inaugurated by the state and national governments. Smith (63) described the general features of the sandhills as to topography and plant distribution. In this paper the writer called attention to the occupation of the slopes by the bunch-grasses, and to the presence of blow-out grasses in their characteristic habitats. A list of grass species with notes as to their occurrence and economic relationship adds to the value of this important early paper.

The decade from 1890 to 1900 saw the publication of a number of important papers that had considerable bearing upon the vegetation of this region. Webber (75) contributed an "Appendix to the Catalogue of the Flora of Nebraska," which included additional sandhill species. Smith pointed out (63) certain relations between the sandhill flora and that of the surrounding prairies, plains, and foothills, and commented upon the richness of the aquatic flora of the region. Among his lists occur grasses of "dry hills," of "valleys and meadows," of "boggy margins of water holes," and of "hay meadows." Bessey (12) discussed the past and present vegetation of the hills especially as related to arborescent species and included a pressing recommendation that something be done toward reforesting the region. Smith and Pound (64) contributed a paper dealing with topographic and drainage conditions and general life relations in the sandhills, and pointed out some of the salient features of wet and dry valleys. Rydberg, as a field agent of the Division of Botany of the United States Department of Agri-

culture, made a study of the flora (58) of that portion of the region lying in Thomas and Hooker counties between the Middle Loup and Dismal rivers, and the eastern portion of Grant County. We have in this paper the most extensive collection of floristic notes from the sandhills that had been gathered up to that time. Rydberg described blow-outs and indicated in a general manner the vegetative cycle that is so characteristic of these habitats. Bessey (17) discussed the question of the migration of the trees and larger shrubs of Nebraska (16), some of which have entered the sandhills from the east and others from the west. Pound and Clements first recognized, in the Phytogeography of Nebraska (57), the natural vegetation regions of the state. The sandhills were here included for the most part within the "Loup District" of "Region III." The vegetation of the sandhills was treated under (1) the bunch-grass "formation" with two subdivisions, the blue-stem "type" and the beard-grass "type," (2) the blow-out "formation," and (3) the sand-draw "formation." The general nature and composition of these "formations" and "types" were given at considerable length. On the whole this general survey represents the most careful attempt at an ecological analysis of the vegetation of the state that has been compiled and should serve as a valuable guide and working basis for detailed work upon the natural plant cover of any portion of the state. The Phytogeography has been of constant service to me during the progress of this investigation and I have drawn from it to a considerable degree in certain portions of this study. The same authors later (56) added certain notes in regard to the position of the sandhills within the "prairie province" and commented upon the endemic nature of the flora of the region. In this paper the contrast between turf builders and bunch-grasses was emphasized.

Soon after 1900 the agitation for reforestation began to bear fruit and in 1903, after an examination of the region by government officials, the national government began the planting of coniferous stock upon the sandhills. At the same time a nursery for the production of stock suitable for planting was established in the valley of the Middle Loup River two miles west of Halsey in Thomas County. Various extensive forestation experiments have been inaugurated by the Forest Service at this place in the attempt to discover if it is possible to cover the sandhill uplands with trees. The government has shown conclusively that certain coniferous species may be grown upon the hills, but it can not be said that it has been

proved that forests of commercial value can be produced over these uplands. It may be that with many more years of experimental study a method may be discovered that will make the production of a crop of trees in the sandhills a surety and a profitable means of utilizing certain areas within this region. As a result of these activities there have appeared a number of publications bearing directly upon the above problems and indirectly including certain more or less fundamental relations that exist in connection with the native vegetation of the sandhills. Bates (3) dealt primarily with the problems involved in the establishment of a forest cover in the hills, but among his studies he included the determination of certain ecological factors and their relation to the native and introduced vegetation. This author recognized four principal "types" in the region about the Halsey nursery. They are ridge, bottom, north slope, and south slope. The different ecological conditions in these types were briefly studied and compared and were found to bear a rather important relation to the forest-planting operations and to the success that was secured in certain experiments. Kellogg studied the forest belts of western Kansas and Nebraska and published observations (44) that are of certain interest especially in reference to the woody vegetation of the stream courses of western Nebraska. Wolcott (77, 78) has shown something of the inter-relations of the flora and fauna in the various regions of the state including the sandhills. Warren published a brief paper (69) in which he told of the abundance of certain leguminous species at a few stations in the sandhills of Nebraska. The same writer included with an agricultural survey of the state (70) considerable general data in regard to the soil and climatic conditions in the sandhills, and commented briefly with reference to certain forage problems. The paper, although of a distinctly agricultural nature, contains some valuable ecological data of state-wide interest. Certain forage problems were studied by Vinall (68) who conducted a number of coöperative experiments with ranchmen of the region in the hope of finding some means of supplementing the natural forage yield. More or less successful experiments were tried with such forage crops as alfalfa, sweet clover, orchard grass, western wheat grass, millet, brome grass, sorghum, etc. Shantz, working mostly in the Great Plains Area of Colorado, investigated (59, 60) the possibilities of determining the capability of land for crop production with especial reference to soil water as this might be indicated by the natural plant

cover. He has pointed out very clearly that when the native vegetation of the Great Plains Area is well understood as to its composition and water requirements, one may conclude rather definitely as to the probable success when various cropping systems are attempted upon this land showing one or another of the common plant associations. This paper is of particular ecological interest in connection with the studies of the sandhill vegetation of Nebraska. Certain comparisons between these regions will be recorded in the following pages. The last papers that deal with sandhill vegetation and related conditions are by myself (53, 54) and are of a more or less popular nature.

This investigation has been conducted under the direction of Professor C. E. Bessey, and I am pleased to express my appreciation of the aid and kindly counsel which he has so freely given during the progress of the studies. Professor F. E. Clements, of the University of Minnesota, has offered criticism and suggestions, and I am especially grateful to him for having read the first draft of this paper. I am indebted to Professor G. E. Condra for guidance in the study of the physiography, soil conditions, and drainage of the sandhill region. Thanks are due the Reverend J. M. Bates for aid in the determination of certain sedges. I am also indebted to the Nebraska Conservation and Soil Survey for help that made possible the extension of my studies over a wide territory. I wish furthermore to acknowledge my indebtedness to the United States Department of Agriculture, Bureau of Soils, for the determination of the mineral content of certain soil samples and for mechanical analyses of sandhill soils which will be found among the following pages. Finally I wish to express my appreciation to the United States Department of Agriculture for permission to reproduce certain figures from Bulletin No. 213 by Dr. H. L. Shantz, of the Bureau of Plant Industry, and to the office of Alkali and Drought Resistant Plant Breeding Investigations for the determination of the moisture equivalent of certain sandhill soil samples.

AREA AND POSITION IN THE STATE

Until a detailed soil survey of the state is completed we can not tell except approximately the total area of our sandhills. Estimates varying from 15,000 to 24,000 square miles have been published by various investigators (Barbour 2, Darton 33, Condra 28, Bessey

16), but studies have gone far enough that we may now chart with approximate accuracy the limits of the main region of sandhills as it occurs in this state. Obviously it is a mistake to include within *sandhill areas* stretches of land characterized by widely isolated sand ridges and ranges of low sandhills because the greater area of such tracts is not composed of dune material but is of a firmer, finer texture and should therefore be included in other soil regions. Parts of Holt and Chase counties with much agricultural land have been treated in this manner. In Dundy, Chase, and Hayes counties there are areas with conspicuously sandy soils, but there is little else to remind one of the typical central sandhill conditions. Even the occasional blow-outs of Dundy County are profoundly modified because of a considerable admixture of hard material with the sand that results in the development of low spires, domes, tables, and other bizarre land forms where such soils are eroded by wind and water. Even with a very conservative estimate of the total sandhill area of Nebraska at 18,000 square miles this means that we have as much as 11,520,000 acres of this sort of land within our borders.

Prominent sandhills are known to occur over the trans-Mississippi country in Kansas, Colorado, Nebraska, and the Dakotas. The largest single area is to be found north and west of the central portion of Nebraska. This main body of sandhills is oblong in shape with its longer axis parallel with the east and west axis of the state and with a center in Thomas and Hooker counties. The margin is very irregular especially toward the eastern limits of the region. The frontispiece map will convey at a glance the position of this main body of hills as well as portray its relative area and form. Besides the main sandhill region there are numerous other much smaller areas of sandhills found in various parts of the state. Some of these minor regions exhibit certain vegetative and topographic characters that resemble those features of the main body, but as a rule such isolated areas are considerably different as to vegetational and other surface features. The more important examples of such outlying areas are to be found in Perkins, Chase, Dundy, Hayes, Lincoln, and Sioux counties as well as at a few small stations near the Platte River farther eastward. Some of the smaller sandy areas are to be included with phytogeographic subdivisions quite different from the typical sandhills.

GEOLOGY AND SOILS

The sandhills are underlaid by a series of geological formations which are probably continuous (Darton 33, Barbour 2, Condra 28) beneath the entire state. The oldest geological formation exposed in Nebraska is the Pennsylvanian (Carboniferous). This series, composed of limestones and shales, is of great thickness and it furnishes products of considerable value in reference to certain indus-

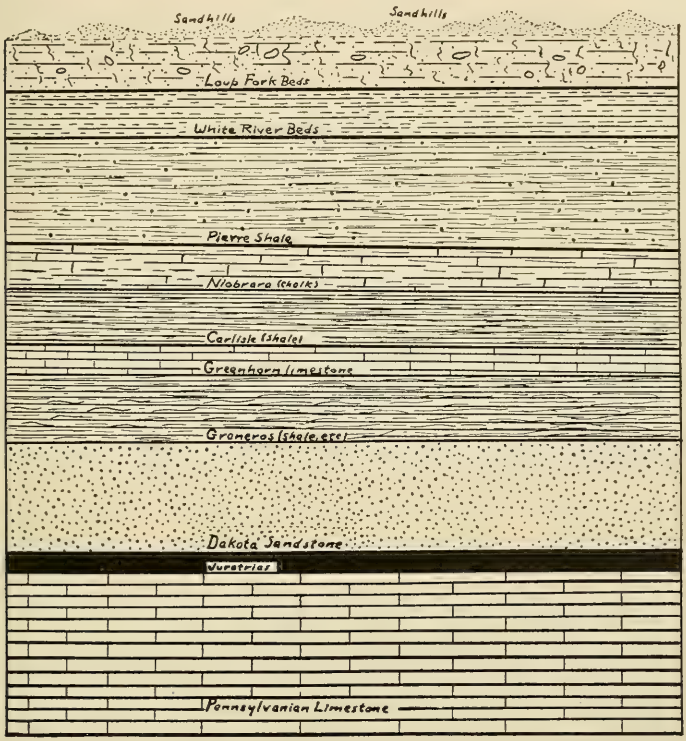

Fig. 1. Vertical section showing the bed rock. This somewhat idealized section is intended to show the relation of the sandhills to the underlying rock series. (Generalized from Barbour, Darton, etc.)

tries of the state. Lying upon the Pennsylvanian series is a thin bed of Jura-Trias. Above this bed comes in regular order a thick stratum of the dark, rusty-red Dakota (Cretaceous) sandstone which also yields commercially valuable grades of building stone. Above this lowest sandstone there lies next in order the Graneros which is mostly shale. Upon the Graneros lies a thin bed of Greenhorn limestone, and this in turn gives way toward the surface to an-

other thick bed of shale known as the Carlisle. Above the Carlisle lies a rather thick bed of Niobrara chalk (Cretaceous). As we continue upward in the series we next reach beds of Pierre shale. The Pierre shale is covered by the White River Beds (Eocene) which vary as to their composition, but include both clays and sands. The Brule clay is one of the best known constituents of the White River Beds. This clay of a very tenacious nature forms extensive outcrops in western and northwestern Nebraska and in South Dakota (Barbour 2) and has been eroded into those fantastic forms known as the "Bad Lands." Upon this series of clays and sand were deposited large quantities of gravel, sand, silt, and clay washed from the western mountains into bodies of water that probably once covered all of western Nebraska. This material has entered into the construction of what geologists have called the Loup Fork Beds (Tertiary). These are now exposed in western Nebraska and apparently most of the present soils west of the sandhills have been derived at least in part from these beds. Thus we see the state is underlaid by a rather complex series of bedded rocks which is probably hundreds of feet in thickness. All of these beds dip slightly toward the east.

The mantle rock, or that material that now characterizes the surface of the state, may be divided into four general classes. Over the eastern portion is a mixture of glacial drift and loess, the one a coarse soil containing bowlders, gravel, sand, and clay, the other a very fine soil composed of silt, clay, and fine sand. The sandhill region is characterized by the presence of dune sand. The region west of the sandhills shows a surface soil light in color and of a rather fine texture somewhat like the loess of the eastern portion of the state although not so uniform as loess, and it is probably of different origin.

The sandhills lie directly upon the Loup Fork Beds as a rule and geologists are agreed that the weathering of the rocks of this series has given the bulk of the material of which the dunes are composed. That such an origin is probable is seen even to-day where outcrops of the Loup Fork Beds are subjected to erosive forces. These rocks weather readily into a rather fine straw-colored sand which is readily blown about by gusts of wind that strike beneath eroding cliffs and canyon sides.

The dune sand in the main region of the sandhills covers the Loup Fork Beds to a depth probably not to exceed 100 feet in any

portion of the hills, and in many places the depth of the dune material is not nearly this great. At many widely distributed places the Loup Fork series is seen in outcrops. Some such outcrops are extensive along certain stream valleys. The numerous spring branch tributaries of the Niobrara that lead out from the sandhill region have eroded very deep canyons in many places. In such places vertical walls of this rock series capped by sand dunes are common and striking landscape features.

A soil composed of quartz sand developed from the erosion of the rocks of the Loup Fork Beds is then the characteristic substratum for the vegetation of the sandhills. Other minerals besides quartz that are common in these soils are magnetite, orthoclase, hornblende, oligoclase, epidote, biotite, apatite. This soil, with an extremely high proportion of insoluble inorganic matter and a very low content of nutrient materials, is about as sterile as could well be imagined. In the larger and deeper "pockets" or basins of the upland and in the valleys of the region the soil becomes a sandy loam possessed of quite different physical and chemical properties and may be made to yield valuable products. Within certain habitats, notably in the river thickets and in some of the numerous upland thickets as well, there is a copious admixture of organic remains so that the upper soil becomes a rich black sandy loam and is fertile.

TOPOGRAPHY AND DRAINAGE

As one views this great sandhills domain for the first time he is inclined to feel that there is little or no fixed or definite form of arrangement exhibited by sandhill topography. However, the land forms here are for the most part those that characterize dune regions everywhere whether over a small territory or an extensive stretch of country such as we have within our sandhill region. Wind blown sand, if present in sufficient quantity, tends to become arranged in the form of hills and ridges whose forms and gradients of slope vary with the age of the hill, the amount of sand available, and the influence of the vegetative cover or other obstacles.

The surface features of the Nebraska sandhill areas vary to a considerable degree. In some portions of the main body of sandhills, as in Thomas County, the individual hills are round-topped, or conical and smooth, if such perfect forms have not been modi-

fied by the development of blow-outs since the dune sand has become more or less perfectly stabilized by invading vegetation. Commonly such hills are more or less united into irregular ranges or ridges with numerous saddles and summits and short lateral spurs.

The depressions between the individual hills of a given range or between the hills of contiguous ranges, vary from narrow bowl-shaped basins or "pockets" a hundred yards in diameter to valleys or meadows with relatively flat floors often more than a mile wide

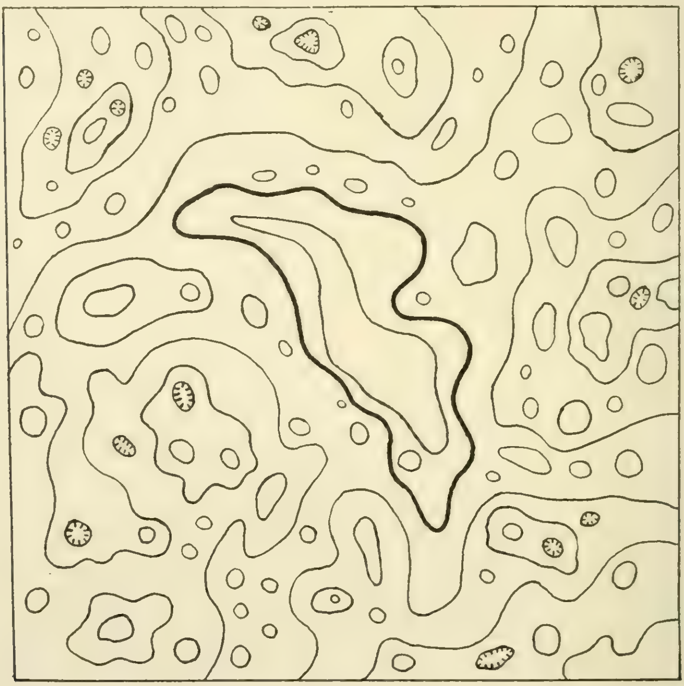

Fig. 2. Topographic features. A square mile among the "choppy hills." Contour interval 20 feet. (Somewhat idealized.)

and sometimes several miles in length. The ranges of hills with the alternating valleys and meadows are as a rule about parallel and trend in a general, more or less irregular, northwest and southeast direction. Such conditions as these are very common especially in the northern portion of the region. I am fully aware, however, that in certain other portions (as in Garden County) this typical valley and range trend is not so clear or constant, and there are here very well-developed valleys which take a different course. Single valleys

are usually not continuous for long distances, unless such a valley be the position of a stream. Meadows and valleys are frequently completely enclosed by ranges of hills and in this way effectively separated from adjacent valleys although such may not be more than a half-mile distant over a low saddle or ridge. In other cases adjacent valleys are united by their ends or sides so that in some parts of the region one may travel for many miles over the firm soil of the valley floor by simply angling from one valley around a spur or end of a range of hills into another valley. High spurlike promontories often extend from the main range of hills into the valleys from the sides. This condition results in the production of a very irregular boundary line for many valleys. Oftentimes the sides of the hills or ridges are very steep, thus making difficult, or nearly impossible in some instances, the direct lateral passage from one lowland area to another. Where broad valleys are the rule, the ranges of hills often reveal a succession of higher hills as one passes back from the valley to the highest points on the divide. This divide may be as high as 100 to 250 feet above the valley floor. Along the northeastern limits of the region low, tortuous ranges of hills separate broad, fertile meadow lands whose soil when "broken" yields abundantly of various field and cultivated forage crops. But in those portions of the hills characterized by very short dry valleys and basins the general topographic conditions are strikingly different because in such places the hills rise on all sides without the customary regularity of distribution into lengthy ranges. Even the general typical east and west trend of the hills is difficult to discern in many such places. Low hills, intermediate hills, and high hills are closely associated in every direction and there are consequently no prominent dissecting valleys. The result of this type of hill distribution is the production of a very abruptly rolling surface with considerable relief consisting of short, oblong, or rounded depressions of varying depth with the rounded or conical dunes above. Such hills frequently bear many of the characteristic blow-outs. The highest hills are usually of a nearly uniform altitude but occasionally one sees a giant hill that towers above the others to such a degree that it has received a local name such as "Plummer's hill" on the Dismal or "Cowboy hill" in Morrill County. The ranchman designates this condition as "choppy hills." There are places where this sort of topography stretches in all directions as far as one can see.

The general altitude above sea level of the sandhill region varies

from about 1,800 feet along the eastern border to about 4,000 feet across the western portion. The places of greatest relief in the region are in the gorges of the Dismal and Snake rivers where the surface of the stream which has cut far into the Loup Fork Beds lies from 300 feet to 380 feet or possibly more below the crests of the highest near-by hills. The Snake River canyon is in some portions characterized by almost perpendicular cliffs capped by enormous hills.

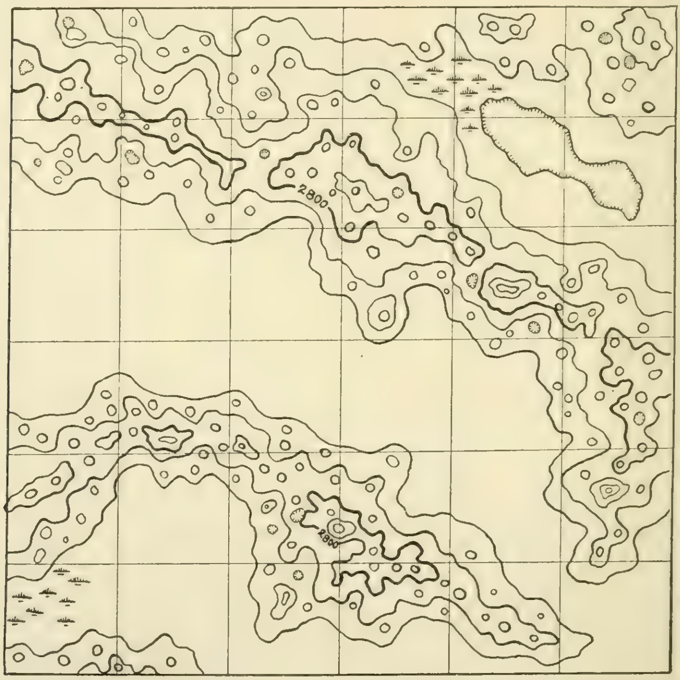

Fig. 3. Topographic features. A township within the hay meadow region. Note the broad valleys and ranges of hills. Contour interval 20 feet. (Somewhat idealized.)

The sandhills are characterized by sub-surface drainage. The loose porous dune sand of the uplands soaks up precipitated moisture very rapidly so that after the heaviest falls of rain scarcely any water is drained from the surface but all of it sinks quickly into the open soil. The soil is quick to lose its water by percolation to deeper levels, thus leaving a minimum quantity permanently in the capillary zone. But a short time is therefore required after even a heavy rain for the penetration of the moisture to a depth below the

reach of the roots of most sandhill species of plants, and they are then in little better condition than before the rain came so far as capillary water is concerned. The usual heavier rains varying in amount from 1 to 2 inches are thus completely taken up by the soil and no surface drainage results. Occasional heavier rain storms, however, produce considerable run-off.

The streams and lakes of the sandhills seldom, if ever, show an increase in volume immediately following even the heaviest downpours. Knowing that run-off is practically nil for the region, one can not fail to appreciate the very gradual but constant delivery of these volumes of water via subterranean routes until it finally reaches the streams and lakes through springs. Fluctuations of this ground water from season to season, however, produce noticeable variations in the delivery of water to springs and consequently also in the level of the surface waters of the region. Numerous intermittent lakes owe their nature to this condition. Variations of this sort are not so evidently reflected in the volume of the swiftly moving streams as with the ponds and lakes. There is a well-known alternation of periods of a few years each when there is considerably more precipitation with other less moist periods which are commonly known as "dry seasons." The level of the water in many of the lakes has been reported to vary through this cycle.

The most important stream of the sandhill region is the Loup River, the three branches of which, the North Loup, the Middle Loup, and the South Loup, rise in marshy flats toward the central portion of the region. These streams flow in a southeasterly course and unite east of the sandhill region to form a single stream which farther eastward pours into the Platte near Columbus. Of these three branches the North Loup carries the most water, while the South Loup, with the shortest course, is characterized also by the least volume. Through the sandhills portion of its course the Middle Loup is reported (58) to have a fall of about eight feet per mile and hence develops considerable velocity. The channel is continually shifting its position in the narrow valley and the river wanders back and forth across the flood plain. Many of these meanders eventually become separated from the channel as cut-off lakes or ponds.

The Dismal River is an important tributary of the Loup from the south. Heading from two points in the marsh and lake region of Hooker, Grant, and McPherson counties, this river continues

eastward for about 75 or 80 miles and empties into the Middle Loup at Dunning. This is the only stream of any size, then, that has its origin and completes its course wholly within the sandhill region.

The Dismal has cut a deep canyon in a number of places along its course extending from the high, steep hills upon either side far below into the more resistant Loup Fork Beds. The sides of this

Fig. 4. Topographic features. A township within one of the lake centers. Note the lakes, marshes, meadows and ranges of hills. Contour interval 20 feet. (Somewhat idealized.)

canyon are sometimes almost perpendicular, while elsewhere the banks are not so wide or precipitous and then more or less covered by trees and other woody vegetation. Almost inaccessible jungles exist in the moister years along the Dismal in the heart of the sandhills. Now and then the stream leaps over a ledge of rock in its bed producing a waterfall a few feet in height. Where the course is more open, the Dismal has produced many meanders and cut-offs.

In addition to the Dismal, the Calamus is an important tributary of the Loup River coming into the North Loup from the northern portion of the region.

The Loup River system thus constituted is the only important drainage outlet from the sandhills to the south or east. Blue Creek in Garden County is a small, clear stream which drains a small portion of the region toward the southwestern limits. To the north, however, there are numerous short streams of considerable volume which rise in the sandhills and follow a northerly course to the Niobrara River. The latter river, the second stream in the state in size, skirts the sandhill region on the north. The tributaries from the south are mostly of the nature of the "springbranches" of Pound and Clements (57). The largest and most important tributary of the Niobrara is the Snake River. This stream rises in eastern Sheridan County and flows eastward through the sandhills parallel with the Niobrara for two thirds of the distance across Cherry County, then turns abruptly northward and finally meets the Niobrara about twenty miles west of Valentine. Along portions of its course this river has cut a deep gorge into the underlying bed rock. The river bed is here very uneven and the fall of the stream great so that in those portions the stream is turbulent and swift and characterized by rapids and falls after the nature of a piedmont or mountain stream.

All streams of the sandhills exhibit a remarkably even flow of clear water. During extremely dry seasons when the precipitation falls below normal and when evaporation is excessive, the volume of these streams is said to vary considerably. Ordinarily, however, the water table is rather high and there is an abundance of water delivered from the sand to the innumerable large springs that characterize the headwaters and the courses of all the streams, so that one of the most striking features of the sandhills is the remarkably uniform flow of their rivers. Some of the feeding springs of the Dismal are noteworthy for their large delivery and because of a distinct rumbling noise as the water boils up in a basin sometimes a yard or more in diameter and to a height of several inches above the margin of the basin.

Many lakes and ponds occur in the sandhills in a number of scattered "lake regions." These lakes vary from small ponds a hundred yards across to a mile or more wide, and from one to five miles in length. Although a number of the lakes are of large size they all agree in that they are relatively shallow. Aside from a few deep holes the average depth of water over the rather even bottom varies from three to six feet. Probably none have a depth

at any spot to exceed fifteen feet, although Blue Lake in Garden County is said to be very much deeper than this.

The lakes of the sandhills occupy narrow valleys or portions of broader valleys. Well-defined groups of lakes, characterized by the presence of a number of larger sized lakes and numerous smaller ponds and marshes of various ages, occur in eastern Cherry County; southwestern Cherry County at the headwaters of the Middle and North Loup rivers; central Brown County; southwestern Holt County, feeding streams whose union gives rise to the Elkhorn River; at the headwaters of the Dismal River in Grant and McPherson counties; in north central Garden County above Blue Creek; and a group of quite alkaline lakes and ponds in southern Sheridan County. The largest lakes are to be found in the Cherry County and Garden County groups among which Dad's, Hackberry, Willow, Big Alkali, Red Deer, Dewey, Crescent, and Blue lakes are the best known. While in a number of cases streams arise from a lake center, yet it appears that in no case does a lake or a lake group possess a direct surface outlet by way of such streams. The drainage is typically subterranean and usually through an extensive series of springs and marshes. There are often many large surface springs along the upper courses of such streams.

There is abundant topographic and other evidence to indicate that in some of the lake centers a number of the lakes that are now rather widely separated were at one time united into one large body of water which occupied adjacent valleys. The old shore line of such lakes is indicated by the margins of the present closely associated or tributary valleys and wet meadows.

GENERAL PLANT-LIFE CONDITIONS

Climatic and Soil Factors

As various writers have pointed out (24, 25, 26, 27, 30, 31, 36, 37, 50, 51, 57, 60) the flora of a sand dune area consists partly of plants especially adjusted to meet the rigors of sandhill conditions, and partly of species found sometimes with greater abundance in other associations, but whose successful responses under the new conditions have enabled them to tolerate the vicissitudes of a dune environment. This quality that I may term dune-tolerance is possessed to a greatly varying degree by different species. This difference enables us to classify certain species of plants as pioneers in

dune reclamation or those in possession of the highest degree of adaptation to a dune environment, and those that are secondary invaders that come in only when the severity of environmental forces has abated to a certain degree. Finally there are species that are very late in establishing themselves upon the dunes, which species we may characterize as possessed of a low degree of dune-tolerance. Then there are many whose absolute inability to invade the dunes results in the development of the quality that might be termed dune-avoidance.

The conditions surrounding the plant-life of a dune area are usually extremely severe irrespective of whether the area is found within a humid or arid climatic subdivision of the earth's surface. In all such places these conditions bring about a series of desert or semi-desert phenomena. On the wind-swept ridges and slopes we find species possessed of varying degrees of wind-toleration. Where wind denudation is absent or has been greatly reduced we find less wind-tolerant species, and in protected basins or valleys, we find certain shade-loving and wind-avoiding species. Wind, then, is by far the most important and constant climatic factor characteristic of dune regions. The sand dunes, and the dune complex as well, are commonly oriented in a definite manner with reference to this force.

The ecological nature of sand combined with the telling influence of wind in the production of environmental conditions for plant life has been described by many writers, notably Cowles (30), Gerhardt (36), Cockayne (26), Hitchcock (41), Olsson-Seffer (51), Cornish (29), Warming (71), and others. It is unnecessary in this place to enter into a lengthy discussion of this matter.

The real destructive action of the wind in these sandhills is not ever-present. Many days are as calm and free from sand movement as one could wish, but at other times, and for periods of several consecutive days, the wind velocity is high and soil dissemination is excessive. In other words excessive wind erosion and destruction are not a constant character of any dune area. For this reason figures that exhibit the total wind velocity for a given period are misleading. The graphs herewith included will nevertheless indicate something of the relation of this factor to the development of a plant cover upon different situations. The graphs indicate the total wind velocity by twelve-hour day and night periods for four habitats through an interval of twenty-one days. During

the time that the anemometers were operated there were days when the instrument placed on the blow-out rim indicated an hourly velocity much higher than this figure. Single hours during especially windy days showed a velocity varying from 35 to 60 miles per hour at this station.

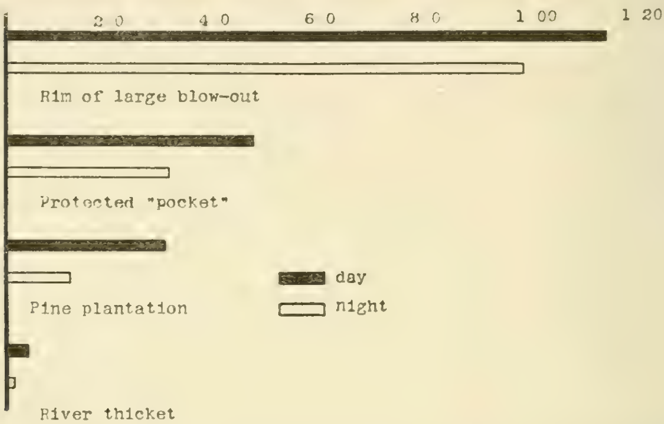

Fig. 5. Wind velocity. The graphs represent averages of 12-hour periods for 21 days.

A phase of wind action that must not be overlooked is related to prairie fires. The region is subject to thunderstorms during the spring and early summer months. These storms are usually accompanied by much lightning which is often responsible for the kindling of prairie fires. Fires are also started near railways by "live" cinders from passing locomotives. Occasionally numerous other sources of origin result in the initiation of these conditions. Irrespective of the origin of a prairie fire, if the wind is high at the time and fire-fighters few, as is usually the case, the fire frequently becomes of uncontrollable proportions. Driven by a powerful wind such a fire may sweep for miles across the hills and may sometimes burn over thousands of acres. The immediate destruction of the range is not the only damage done by such a fire. It may happen after the fire has swept the uplands free of vegetation, that the wind striking now upon the exposed sandy slopes results in the rejuvenation of blow-outs and of general maximum sand movement so that the grazing value of the area burned is reduced to an extremely low figure for many years.

The main sandhill region of the state may be said to lie within

the transition belt between the eastern humid climatic conditions and the western arid or semi-arid climate that characterizes the great plains between the one hundredth meridian and the foothills of the Rocky Mountains. There can be little doubt that the summation of semi-arid or arid characteristics that are revealed within this region have exerted a very powerful influence upon the maintenance of the general vegetation characteristics of the sandhills for untold years essentially as we find them to-day.

The normal precipitation in Nebraska varies from about 36 inches in the southeastern corner to 15 or 16 inches toward the extreme western end of the state. This is through an interval of

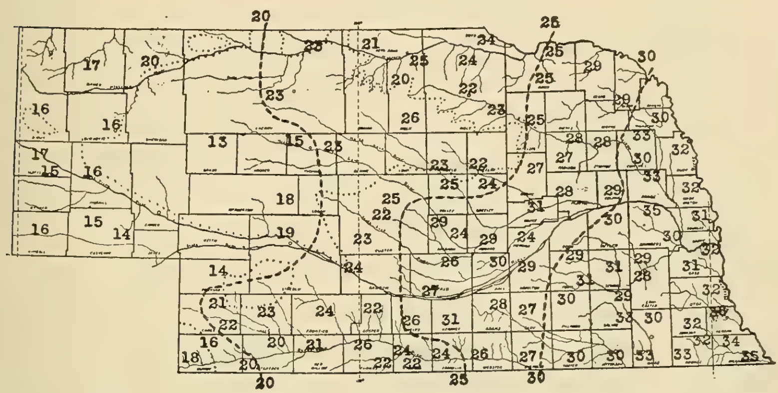

Fig. 6. Rainfall map of Nebraska. The figures show the normal rainfall in inches. (Adapted from Briggs and Shantz.)

more than four hundred miles. Briggs (19) and Belz have made an extensive study of dry farming in the United States as related to rainfall and evaporation. Figure 6, which I have adapted from these investigations, portrays at a glance the above precipitation wave as it sweeps from east to west across the state. These figures which have been compiled from the records of the United States Weather Bureau show that the rainfall for the sandhills varies from about 23 inches on the eastern border to about 16 inches near the western limits through a distance of about three hundred miles. The intermediate position between relatively humid and arid conditions is thus very clearly indicated. The normal precipitation at various stations within or near the sandhills is shown in the following table which has been extracted from the extensive precipitation table for Nebraska published by Briggs and Belz (19).

NORMAL PRECIPITATION AT STATIONS WITHIN OR NEAR THE SANDHILLS

Station	County	Length of record	Normal precipitation
EASTERN BORDER			
Bassett	Rock	6 years	20.10 inches
O'Neill	Holt	11 "	22.20 "
Burwell	Garfield	17 "	23.10 "
Halsey	Thomas	7 "	23.40 "
Callaway	Custer	12 "	22.70 "
			Mean: 22.30 "
CENTRAL PORTION			
Valentine	Cherry	21 years	22.50 inches
Seneca	Thomas	7 "	14.80 "
Kennedy	Cherry	16 "	23.00 "
Whitman	Grant	11 "	13.30 "
Nesbit	McPherson	7 "	17.90 "
			Mean: 18.30 "
WESTERN BORDER			
Hay Springs	Sheridan	22 years	20.10 inches
Alliance	Box Butte	11 "	16.40 "
Agate	Sioux	7 "	15.70 "
Bridgeport	Morrill	13 "	16.10 "
North Platte	Lincoln	35 "	18.90 "
			Mean: 17.44 "

Soil-moisture is a very important factor in regard to the local distribution of species and plant associations. Notwithstanding the fact of rather great differences in rainfall at widely separated stations within or near the sandhills, soil-moisture does not appear to present nearly so great a range in quantity as might be expected. Quite apart from the precipitation, it is uniformly the rule that at a depth of but a few inches below the surface of the sand, even in the most exposed situations, and in the driest portions of the hills, the sand is moist; so moist in fact that at a depth of one foot or less I have seldom found soil in the sandhill uplands during my extensive travel through the region, so dry that it could not be moulded in the hand. Whether this is due to capillarity alone, or as Jentzsch (42) has shown, in part to an internal dew formation within the dune, the fact remains that moist sand is always found at a depth of a few inches. The great variations of diurnal and nocturnal temperatures *may possibly* effect periodical condensation of the water vapor held in the upper layers of sand and thus aid in the maintenance of a reservoir of water near the surface.

As has been said precipitated moisture is absorbed at once by the porous soil and such rain water descends to a depth varying with the texture of the soil. Evaporation, as soon as the storm passes, results in a drying of the surface with great rapidity, but this is only to a slight depth. The loose sand acts as a dry mulch to check evaporation from greater depths. The rate and ease of water

movement either by capillarity or percolation through a soil depend upon the coarseness of the particles. We have already seen that sand movement under the influence of the wind depends upon the same factor. Even after a prolonged period of drought, moist sand is sure to be found within four inches of the surface.

A relation overlooked by most students of dune phenomena is that, while moisture so near the surface aids considerably in resisting wind erosion, yet under prolonged drought conditions this resistance is quite readily broken up. At periods with the prevalence of extremely high winds and low saturation deficit, the surface level of exposed situations upon the dunes is rapidly lowered because of the relatively rapid rate of depression of this moist layer.

The soils of which the dunes of the Nebraska sandhills are composed is made up of particles of widely varying dimensions. The accompanying table shows the results of mechanical analyses of these soils.

MECHANICAL ANALYSES OF SANDHILL SOILS[1]

Station	Fine gravel 2.00 to 1.00 mm.	Coarse sand 1.00 to 0.50 mm.	Medium sand 0.50 to 0.25 mm.	Fine sand 0.25 to 0.10 mm.	Very fine sand 0.10 to 0.05 mm.	Silt 0.05 to 0.005 mm.	Clay 0.005 to 0.000 mm.
Sand from an active blow-out...	0.00	1.20	25.9	66.9	4.70	0.20	1.00
From bare hilltop.	0.20	6.70	21.0	60.2	7.90	2.20	1.60
From among bunch-grasses ..	0.00	5.30	32.1	56.1	5.10	0.30	1.10
Soil from forest nursery	0.40	4.10	9.3	57.1	19.50	7.60	1.80
From river thicket	0.10	3.00	12.6	43.0	22.10	15.10	4.00
From clay outcrop	0.00	0.80	2.5	6.0	6.00	22.20	62.60

[1] Determined by U. S. Dept. Agr., Bureau of Soils, 1913.

The wind can not move large and small sand grains with the same velocity. The size of the grains moved and also the distance to which they are carried varies according to the force of the wind. As a consequence of these facts the wind exerts a distinctly winnowing or sorting action which results in the formation of sand ripples. These sand ripples, or small waves resembling in appearance those formed in shallow water by the sorting action of water, are characteristic of all dune areas. The mechanism of sand ripple formation has been studied experimentally by Cornish (29).

The common conclusion appears to be that sand contains very little available plant food materials. Certain writers, Massart (46), have emphasized this deficiency in the production of the sparse vege-

tation of dune regions. Massart's conclusions were supported by very careful observations and soil-analyses, but it seems that a knowledge of the mere chemical composition of the sandy soil furnishes little indication of its nutritive content. Several ruderal species in our sandhills develop a luxuriant cover in *apparently* sterile sand if certain *soil-moisture conditions* are fulfilled.

Alway and Bishop (1) have made chemical analyses of the soil from many portions of the state including the sandhills and I reproduce herewith one of their tables (somewhat abridged), showing especially the nitrogen content of dune sand from this region.

COMPOSITION OF SOIL SAMPLES FROM SANDHILLS

Depth	Per cent Humus	Per cent Humus ash	Per cent Nitrogen
Surface 6 inches........	...	...	0.027
" " "	0.16	0.53	0.025
" " "	0.18	0.14	0.024
" " "	0.14	0.09	0.018
First foot	...	...	0.024
Second foot	...	...	0.013
Third foot	...	...	0.007

These writers state that "a much higher percentage of nitrogen and humus occurs in the surface soil of the basins and valleys of these sandhills." The comparison of these figures with those secured by the same investigators from prairie uplands in eastern Nebraska brings out rather striking differences.

COMPOSITION OF SOIL SAMPLES FROM PRAIRIE UPLANDS IN EASTERN NEBRASKA

Depth	Per cent Humus	Per cent Humus ash	Per cent Nitrogen
First foot	2.69	...	0.240
Second foot	1.00	...	0.111
Third foot	0.45	...	0.066
First foot	2.90	0.88	0.242
Second foot	1.47	1.40	0.149
Third foot	0.62	0.42	0.069

In some of the valleys toward the eastern limits of the sandhill region and about the headwaters of the streams and near many of the lakes of the region, there are lowlands where silting-in has been accomplished to a considerable degree and where one may pass in a short distance from the practically "pure" dune sand of the uplands to the fertile dark silt loam of an old marsh. Such silty material is, however, rarely more than a few inches in depth and in many

instances is held firmly among the subterranean organs of various marsh and wet meadow plants.

The contour and exposure of the land has considerable to do with the distribution of soil-moisture. The distribution of species and of plant associations is therefore naturally related to these factors. Add to this temperature and the mechanical effect of the wind and we have the most important forces that are brought to bear upon the vegetation of the sandhills. The influence of exposure and depth of soil upon soil-moisture is shown especially well in the following table from Bates' investigations (3).

AMOUNT OF MOISTURE IN SOIL
PER CENT OF DRY WEIGHT

Station	At 12 in.			At 24 in.			At 36 in.			At 72 in.		
	May	July	Sept.	May	July	Sept.	May	July	Sept.	May	July	Sept.
South slope...	4.06	1.94	3.11	4.77	1.62	3.12	4.29	1.78	3.18	3.87	2.75	3.30
Bottom	5.06	2.94	4.72	4.82	2.11	4.18	5.43	3.30	4.21	6.54	7.44	8.56
North slope...	5.11	3.02	4.70	5.26	3.33	5.07	5.87	5.14	6.65	5.88	7.31	7.41
Ridge	3.33	4.01	3.58	4.38	3.79	3.85	5.22	3.67	3.70	5.36	4.18	4.94

It will be observed from the above table that the fluctuation in soil-moisture as the various sites are compared reaches a minimum in July.

The relative retentiveness of different sandhill soils for moisture is determined by comparing the moisture equivalents of the various soils. These values have been determined in the laboratory of the office of Alkali and Drought Resistant Plant Breeding Investigations, United States Department of Agriculture, and are published for the first time in the following table.

MOISTURE EQUIVALENT OF SANDHILL SOILS

Station	Moisture equivalent
Sand from active blow-out	1.37 ± 0.1
Sand from bare hilltop	1.70 ± 0.1
Sand from among bunch-grasses	3.90 ± 0.1
Soil from forest nursery	7.90 ± 0.1
From river thicket	14.60 ± 0.1
Clay from a north slope...........................	43.60 ± 0.2

The value given is the mean of four or more determinations in each case. The number following the plus and minus sign is the probable error in the mean value.

Two other common phenomena that aid in the depletion of the water in the soil, are transpiration and evaporation. The study of the indirect loss of water via vegetation has only been begun and no significant data have as yet been secured for the sandhills of Nebraska. Because of the extensive reconnaissance of the whole

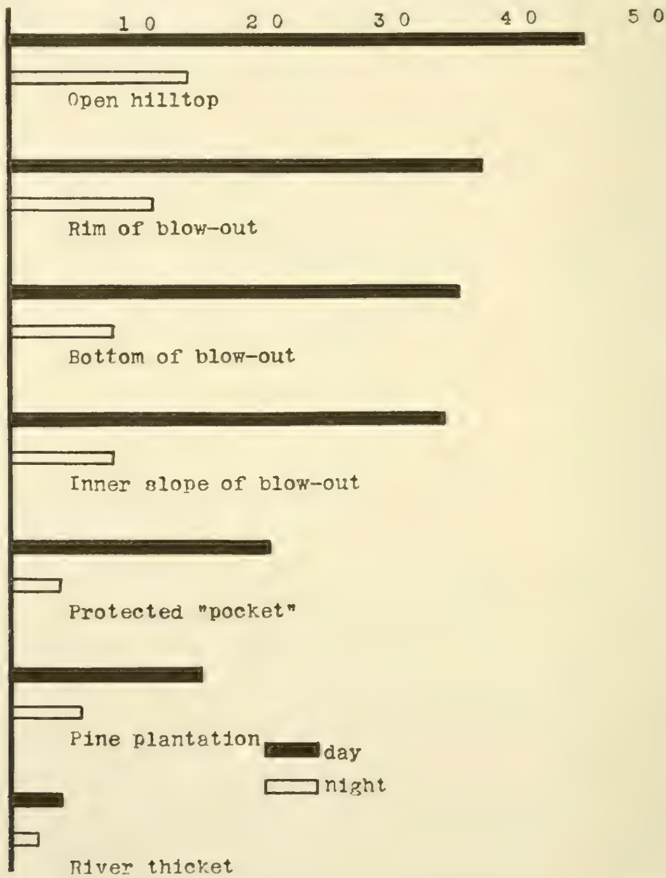

Fig. 7. Evaporation in c.c. from standardized evaporimeters. The graphs represent the average of 12-hour periods for 21 days.

region necessary for the purpose of this report it has also been impossible to obtain a lengthy record of evaporation. During July, 1911, a record of evaporation for twenty-one days was obtained for seven habitats of the region. These records were secured by the use of the porous cup atmometer. The cups used were of the

"standardized coated type" prepared after Livingston's directions and sold by the Plant World. Distilled water was used throughout the study and the several evaporimeters were frequently checked in order that their readings might be compared. The evaporating power of the air as determined by this method for six representative habitats, and also within the densest portion of the Jack Pine plantations in the Dismal River National Forest, is compared in the accompanying graphs, Fig. 7. This month was rather moister than the usual summer months in the sandhills since the precipitation was 5.45 inches[1] during the month. Probably, therefore, the evaporation figures are quite low for the typical conditions. The data are to be regarded as purely preliminary and may be of value with reference to future data of the kind secured within the sandhills and the surrounding territory. These figures bring out striking differences in

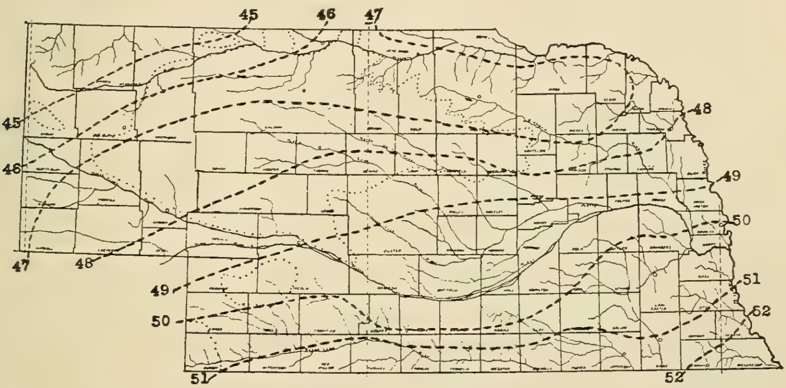

Fig. 8. Temperature map of Nebraska. The isotherms show the mean annual temperature in degrees F. (From Warren.)

the evaporating power of the air in different situations, as for instance that of the open hilltop is more than twice that of a protected basin or pocket only a few hundred yards away. The saturation deficit and the temperature of both air and soil would also be expected to vary considerably through the different habitats. This has also been demonstrated in a preliminary manner. Briggs and Belz (19) give 41.3 inches as the average evaporation (from an open tank) at North Platte, Nebraska, near the southern margin of the sandhill region, for the summers (April to October) 1907 to 1909 inclusive, while at Lincoln the average for eleven years has been 34.8 inches.

A glance at the accompanying map (Fig. 8) will show that the

[1] From the official records of the Forest Service, Halsey, Neb., 1911.

sandhills lie mostly between the isotherms of forty-seven and forty-nine degrees Fahrenheit, and that the region is not therefore the hottest portion of the state. The chart does not, however, indicate in any manner the extreme conditions under which the plants of certain habitats exist during excessively warm days with high desiccating winds that characterize certain portions of the year in the sandhills. Temperature extremes exert a much more powerful influence upon the distribution of life than does the average mean annual temperature. During the vegetative period there occurs in this region a great daily range of temperature both of the air and the soil. After an extremely dry, hot day the temperature may drop to a point that is uncomfortable during the night. Noteworthy diurnal fluctuations in surface soil temperatures have been recorded during these studies. Because of the low specific heat of the dune sand it is found that the surface of the soil over the uplands cools to a low temperature very quickly after sunset and heats rapidly after sunrise. It was found for instance that the maximum surface temperature upon the bare sand for a period of twenty-one days during July, 1911, in the central sandhills was 154° Fahrenheit and the minimum for the same period was 76° Fahrenheit. There were a number of days during this period when the temperature maximum approached to within ten degrees of the above maximum.

Surface insolation is greatly affected by the aspect and by the presence of even a scanty plant cover. A great difference was also recorded between the surface temperature of the soil and the temperature at a few inches beneath the surface in the moist sand. The following table exhibits some of the relationships that exist between these particular environmental factors.

TEMPERATURE OF THE SOIL—JULY 21
(Degrees Fahrenheit)

Depth	In blow-out facing sun	Top of hill among bunch-grasses	South slope among bunch-grasses	North slope among bunch-grasses
Surface	145.0°	121.2°	129.6°	91.5°
Six inches.......	74.5°	72.5°	73.0°	64.5°
Eighteen inches..	66.5°	60.0°	65.5°	62.0°

This table brings out a striking difference between the temperatures at the surface and at a depth of six inches even on the hottest days of the summer. The presence of a rather high amount of capillary water may have a bearing upon this difference. Radiation and reflection is great from the more exposed soils. This is

especially noticeable in certain portions of Garden County where the reflected light is so strong that early eye fatigue results and studies are continued under disagreeable conditions unless one is provided with stained glasses.

The region as a whole is exposed to strong illumination. However it is only in connection with the woodland vegetation and possibly also with certain aquatic and helophilous associations that light becomes an important limiting factor.

Soil-moisture is the controlling factor in the distribution of the lowland species and associations. Silting-in and chemical composition of the soil solution are additional conditions that aid in the differentiation of the vegetation groups of the lowlands.

Although there are at present numerous larger or smaller areas in the sandhills where sand movement is extreme, it must be stated that the region as a whole is effectively protected against wind action by an efficient grassy cover. The region is not a *moving dune landscape* as some suppose! The initial practice in dune reclamation has therefore been consummated through the activity of nature herself without the aid of man, but it appears that man has done little to better the uplands after they have been so well and thoroughly stabilized as a result of the interaction of natural forces. Practical methods for the reclamation and utilization of dune areas have been suggested by various investigators, especially Hitchcock (41), Free and Westgate (35), Poisson (52), and Gerhardt (36).

THE PLANT FORMATIONS

I do not propose to enter here into a lengthy discussion of the general concept or nature of plant formations and associations. This has been done in a number of cases in the literature cited herewith and the reader is referred to those papers for discussions of this phase of phytoecology. The views of Clements (23, 24, 25), Cowles (31), Moss (49), Tansley (65, 66), Jennings (43), and Warming (71) upon plant formations have had the widest test and application.

There can be no question of the fact, as Moss (49) has pointed out, that there has been too great a tendency in the past to elevate minor vegetation units to the dignity of plant formations. Errors of this sort may be readily accounted for in some cases from the

fact that the study in question covered so restricted an area that the student failed to grasp the true significance of the habitats before him. The same careful analysis of the plant cover of a much wider territory might in some such cases reveal the illogical nature of such classifications.

As to the relation between plant formations and associations and succession I am somewhat uncertain, but at present I prefer to speak of the stages of a succession as associations. There is the further possible desirability of establishing the terms "temporary climax," or even "sub-formation," to cover those successional stages that appear to dominate a rather abnormally long period in the development of a given formation.

My own tendency has been to apply the term "formation" to as broad units as possible. I have designated some formations and associations by names that indicate some striking physical character of the habitat, while in others the delimitation is made more easily possible by reference to some dominant vegetational characteristic. A combination of these two phases will be seen in a few instances. Recourse to this method has resulted in the differentiation of plant formations and associations that are reasonably definite throughout the sandhills of north central Nebraska.

I shall endeavor to maintain the now relatively common conception and relation of formations and associations. When I use the term *plant society* I mean to refer to a well-defined area or subdivision of tertiary rank usually characterized by species which become only locally dominant. These species are not included among those which are *formationally* or *associationally* dominant. Furthermore the plant society is sometimes characterized by a conspicuous seasonal appearance.

From the geographical position of the sandhills of Nebraska we might expect to find that the floras of the east and of the west are to be found here existing under more or less equal terms. Lying as they do between great stretches of Prairie Province to the east and the short-grasses of the Great Plains to the west, the sandhills exhibit a remarkable commingling of plants from distant biotic centers whose relationships are mirrored in the vegetation of this inland dune region. Pound and Clements (56, 57) long ago brought out some of these striking characteristics. These writers pointed out that four floral "elements" are represented in the Nebraska sandhills. These are (1) a prairie element invading from the east,

(2) a Mississippi-Ohio valley element, also from the east, crossing the prairie as slender tongues, (3) a foot-hill element whose alliance is westward, or great plains and montane in nature, and (4) a "proper" element or that which the vicissitudes of the region have called into existence. The western montane element is seen especially well-developed along the northern portion of the sandhill region where it is represented by *Pinus ponderosa scopulorum*, a conspicuous species of the hills and canyons where Loup Fork Beds are exposed along the Niobrara River and its sandhill tributaries from the south.

The most powerful or controlling influence here is exhibited by the eastern prairie element. The sandhills of our state appear to present a western type of the vegetation of the Prairie Province existing under the extreme environmental rigors of a dune region. To this must be added the observation that this prairie variation is augmented and considerably modified, first, by the presence of certain species that do not appear in the prairies farther eastward, and, second, through changes in the habits and structure of typical prairie species that have enabled such plants to succeed under the peculiar conditions imposed by a sand dune region within a semi-arid climate.

As would perhaps be anticipated from the intermediate position of the sandhills, it has been found that prairie species decrease in frequence and abundance rather rapidly from east to west, and that the frequency and abundance of Great Plains species rapidly diminish as one passes eastward from the western limits of the region. Two vegetational frontiers are thus seen to meet within the region covered by the present investigation.

UPLAND FORMATIONS

The Prairie-Grass Formation

Under the prairie-grass formation I mean to include all those uplands lying in general between the Mississippi River and the Rocky Mountains that are dominated by grasses of a considerable height and possessed by either the sod-forming or bunch-grass habit. It is appreciated that this is a very broad conception and that the formation thus characterized covers a vast territory and is composed of numerous associations. The Prairie-Grass Formation of this nature embraces practically all of that great stretch of land included within the prairie and sandhill "regions" of Pound and

Clements (56, 57). The former region is characterized especially by the presence of *turf-forming* grasses, the latter by species that have acquired the *bunch-grass* habit.

The chief association of the prairie-grass formation in the sandy portions of the formation, especially where definite sandhills occur, is the bunch-grass association which is to be considered as a *temporary climax* association of the formation in such regions. In those portions of the formation with a more stable substratum (of an argillaceous, loessal, drift, or loamy nature) various associations of long-stemmed grasses possessed of the sod-forming habit predominate. With these we are not especially concerned in this paper although of necessity they must be noted in connection with certain possible successional phenomena.

I wish to insist furthermore that this region is dominated by grass species of a similar physiognomy but at the same time quite different from those grasses that control wide stretches of upland between this formation and the foothills of the Rocky Mountains. As we go westward we find that certain other types of grassland become conspicuous under certain soil conditions and an arid climate. Certain prairie-grasses and short-grasses become associated as alternating associations. This common condition is revealed in various portions of the Great Plains. I wish then to emphasize the desirability of maintaining in our ecological classification a *prairie-grass formation* toward the eastern portion of the Trans-Mississippi region as ecologically distinct from a *short-grass formation* lying between the former formation and the base of the Rocky Mountains. After a rather extended investigation including both areas, the facts of distribution seem to warrant the above conception which appears to coincide with the ideas of Shantz (60) and others who have had an even wider experience in the great belt of grassland stretching from the broadleaf and conifer forests of the east to the coniferous forests of the Rockies.

There can be little doubt, especially after the most admirable work done by Shantz (59, 60), that the two complexes of limiting factors in the differentiation of these two great plant formations are climate and competition. Precipitation and competition are certainly the crucial phases of the problem instead of temperature as Merriam (47) and his followers conclude.

The prairie-grass formation is limited on the east by that combination of climatic and edaphic factors that makes tree growth

possible, a type of vegetation with which the prairie can not favorably compete. Because of the peculiar rigors that the forest frontier meets, tree species invade the prairie sod with extreme slowness notwithstanding the fact that there may be sufficient soil-moisture in such situations for the maintenance of a woodland plant cover partaking of the nature of the Ohio-Mississippi valley forest complex. The prairies quite effectively restrict the westward march of the great hardwoods forest and conversely the forest reduces to a great degree the possibility of the eastward extension of the prairies.

Shantz (60) has contributed evidence to show that within the Prairie-Great-Plains grassland the distribution of the prairie-grass and short-grass formations is clearly a natural delimitation brought about by precipitation and available soil-moisture. The prairie grasses and their characteristic associates can not invade to any great distance the short-grass region because of too low water content of the soil. On the other hand the eastward dispersal of the short-grasses and their associated species is restricted by the presence of deeper-rooted species of the prairie-grass formation which are not only able to hold the ground against, but actually to repel, their shallower-rooted relatives.

The prairie-grass formation as above defined is by far the most extensive type of vegetation within the sandhill regions of Nebraska. Stretching as it does in almost unbroken continuity over the uplands in practically all parts of the hills and extending well down into the drier valleys, the area occupied by the associations of this formation constitutes at least sixty per cent of the total 18,000 square miles. The typical vegetative background of the sandhill landscape is that of a prairie in which the bunch-grasses are the most frequent controlling species.

THE BUNCH-GRASS ASSOCIATION

The bunch-grass association is to be found to a greater or less degree in practically every portion of the typical sandhills, and with the blow-out association is to be considered as the most characteristic type of vegetation within the region. The bunch-grasses are absent from the uplands only where fire or grazing has ushered in one of the associations nearer the initial stage in the succession, or, as on the outskirts of the region and in certain valleys, where sod-forming species become controlling. The bunch-grass association as here

considered is very similar to the "Bluestem Type" of the "Bunch-Grass Formation" of the Phytogeography of Nebraska.

The bunch-grass habit is that aspect of prairie vegetation which, although found in greater or less degree in practically all prairie areas of the United States, has succeeded in a remarkable degree against the rigorous conditions imposed by a very sandy soil and a semi-arid climate.

The frequency and often the great abundance of interstitial species of the bunch-grass association with an unmistakable alliance with the more extensive type of the prairie-grass formation as it occurs farther eastward, constitute additional argument in favor of the conclusion that the bunch-grass condition of the sandhills is merely a variation of the more typical nature of that formation brought about by the ecological conditions briefly indicated upon preceding pages. I therefore prefer to regard this variation as an association of the great prairie-grass formation instead of a separate plant formation as suggested by Pound and Clements (57). From Shimek (61) it appears that this is also the typical nature of the vegetation of the sandhills of Iowa. The facts of succession, as we shall see, also favor this subordination.

The most highly developed and typical expression of this association is found where there is the greatest uninterrupted stretch of sandy upland. Conditions of this sort radiate from Thomas and Hooker counties as a center. Northward from the above defined bunch-grass center the bunch-grass association is soon interrupted and dissected by the numerous wet valleys and meadows with lowland associations that are so characteristic of the Cherry County portion of the sandhill region. Here the association is very sharply bounded through the medium of soil differentiation and the resulting divergence in competition phenomena that distinguish uplands from lowlands which here are very pronounced. Within this portion of its range the association is presented in the form of tongues often miles in length and hundreds of yards across, or of smaller isolated ranges with short spurs and islands with bold faces alternating with narrower lowlands. This characteristic distribution may be quite easily appreciated from a glance at the topographic sketches found elsewhere in this paper. Such dissected nature of the association persists for the most part throughout Cherry County. The tendency appears to be that as one passes outward from the geographic center of this association the lowland area increases and

the uplands become of less extent. This condition is most noticeable as one goes north and east where occur extensive lake and marsh regions as in eastern Cherry County and southwestern Brown County. The increasing proportion of lowlands as the eastern and northeastern limits of the sandhills is approached is very pronounced until, as one finds in southern Holt County and in Antelope County, the typical expression of the bunch-grass association is restricted to the widely scattered ranges of hills that serve as narrow boundaries of wide and flat natural meadows. The most widely isolated spurs of sandhills retain much of their typical sandhill characters for a surprisingly long time.

Toward the southeastern and northern portions of the sandhill region the sandy soil appears to give way more abruptly to the loess region and consequently the distribution of the bunch-grass association is here terminated by a more clear-cut boundary line. Westward the transition from sandhills to the firm soil of the high plains with its short-grass cover is as a rule quickly made and there are few scattered ranges of sandhills on this border that reveal the presence of the bunch-grass association.

The plants that share in the botanical composition of this association as it occurs in the Nebraska sandhills are shown in the following lists of species which are classified into three groups based upon their relative abundance.

Composition of the Bunch-Grass Association

DOMINANT SPECIES

Andropogon hallii
Andropogon scoparius

PRINCIPAL SPECIES

Calamovilfa longifolia
Carex stenophylla
Ceanothus ovatus pubescens[1]
Helianthus subrhomboideus[1]
Meriolix serrulata
Muhlenbergia pungens[3]
Prunus besseyi[1]
Psoralea lanceolata[3]
Rosa arkansana[1]
Stipa comata[1]
Yucca glauca[1]

SECONDARY SPECIES

Acerates angustifolia
Acerates lanuginosa
Acerates viridiflora
Acerates viridiflora ivesii
Acerates viridiflora linearis
Allionia hirsuta
Allionia linearis
Amorpha canescens[1]
Androsace occidentalis
Anemone caroliniana

Anogra pallida
Aragallus lamberti
Arctostaphylos uva-ursi[1]
Aristida longiseta
Artemisia canadensis
Artemisia filifolia[1]
Asclepias arenaria
Asclepias latifolia
Aster multiflorus
Astragalus crassicarpus
Astragalus esculenta
Bouteloua curtipendula
Bouteloua hirsuta
Brauneria pallida
Carduus plattensis
Carex filiformis
Carex marcida
Carex pennsylvanica[1]
Chrysopsis villosa
Collomia linearis
Commelina virginica
Cycloloma atriplicifolium[2]
Cymopteris montanus
Cyperus schweinitzii
Eragrostis trichodes
Erigeron bellidiastrum
Eriocoma cuspidata[3]
Eriogonum annuum
Erysimum asperum
Euphorbia geyeri
Euphorbia hexagona
Euphorbia petaloidea
Froelichia floridana
Gilia longiflora
Ipomoea leptophylla[1]
Helianthus petiolaris[2]
Hymenopappus filifolius
Koeleria cristata
Kuhnistera candida
Kuhnistera purpurea
Kuhnistera villosa
Lacinaria squarrosa
Lathyrus ornatus[1]
Lathyrus ornatus incanus[1]
Lespedeza capitata
Lesquerella argentea[1]
Leucocrinum montanum
Linum rigidum
Lithospermum angustifolium
Lithospermum gmelini
Lygodesmia juncea[1]
Machaeranthera sessiliflora
Oenothera rhombipetala
Opuntia humifusa
Panicum virgatum
Paspalum setaceum
Pentstemon albidus
Pentstemon angustifolius
Pentstemon gracilis
Pentstemon grandiflorus[1]
Phaca longifolia[3]
Phlox douglasii
Polygala alba
Polygala verticillata
Psoralea cuspidata
Psoralea esculenta
Rhus trilobata[1]
Rumex venosus[2]
Salix humilis[1]
Senecio plattensis
Sideranthus spinulosus
Sisyrinchium angustifolium
Sorghastrum avenaceum
Sporobolus asper
Sporobolus cryptandrus
Talinum teretifolium
Thalesia fasciculata
Thelesperma gracile
Tradescantia occidentalis
Vagnera stellata[1]

[1] Forming societies or communities. [2] Becoming ruderal. [3] Relicts.

The uplands characterized by the presence of this association are peculiar because of the growth-form of the dominant species and a number of the commoner interstitials which show various degrees of the same bunch-grass tendency. The individual bunches or tufts of *Andropogon scoparius,* the most frequent and abundant dominant, are composed of from a few to sometimes a hundred or more slender wiry stems with a height ranging from 1 foot to about 2.5 feet. Commonly there are several generations of dead stems to

Fig. 9. Bunch-grass, *Andropogon scoparius,* showing habit of growth, *a*; single plant, *b*; and details of spikelet, *c, d, e, f.* (From Shantz.)

be seen in these persistent bunches that have not been molested by fire for a number of years. The old leaves and culms frequently persist for many years as a dense recurved brush about the individual bunches. The persistent bases of the aggregated stems are rather resistant even when exposed to high winds when the sand may be moved away from the bunches to a depth of several inches so that the bunches stand considerably above the general soil level,

a tendency which all the more influences the conspicuous nature of the bunch-grass form.

Even though there are numerous other bunch-forming plants associated with the dominant species, and in addition to these, a host of interstitials lacking this growth-form, the fact remains that the typical appearance of the bunch-grass association is that of an *open association.* Seldom in the characteristic development of the association is the light-colored substratum hidden from view. The proportion of the ground covered by the bunch-grasses and their numerous associates varies widely with the stability of the substratum. This very often means that such variation is regulated by the age of the association, i. e., the interval that has elapsed since the bunch-grasses originally invaded blow-out areas. In some of the more protected "pockets" which fire has not entered for a number of years and in dry meadows the sand is sometimes very nearly completely covered by vegetation. But in such cases as this we have other dominant species present and the areas have lost their typical bunch-grass appearance.

Apparently the ground cover in our typical sandhill uplands rarely attains to the degree of perfection that Gleason (37) notes for the bunch-grass association on the inland sand deposits of Illinois. Farther westward, as noted by Shantz (60) in Colorado, and on the firmer soils on the borders of the association as it occurs here, the bunch-grasses alone occasionally form a cover sufficiently dense to hide the soil and to inhibit the invasion of many of the secondary species. This state of affairs naturally approaches the conditions typical for other associations of the Prairie-Grass Formation. Toward the opposite extreme in the developmental series the bunch-grass association becomes more open and the bunch-grasses less dominant and the association then approaches the blow-out association.

The bunch-grass of widest distribution and of most frequent controlling influence is *Andropogon scoparius.* There are, however, other grasses of wide distribution possessed of similar growth-forms. These seldom occur in sufficient abundance to lend a conspicuous color to the association, much less become dominant. The species that may become locally important in this manner are *Andropogon hallii, Calamovilfa longifolia, Stipa comata, Koeleria cristata, Eragrostis trichodes,* and *Eriocoma cuspidata.* The latter two are more closely associated with the blow-out association. When these

species occur within the bunch-grass association they are therefore to be regarded as relicts. Indeed these species do not always present the bunch-grass habit, and whenever this tendency appears the bunches are small and the number of component stems much fewer than is the case with *Andropogon scoparius*.

At stations in the central and eastern portions of the hills these

Fig. 10. Big bluestem, *Andropogon hallii*. Clump, showing habit of growth, *a*; single plant, *b*; details of spikelet, *c, d, e, f*. (From Shantz.)

species become (as reported by Pound and Clements) locally controlling at certain seasons of the year. Thus during early summer the bunch-grass association may be quite distinctly modified by the presence of *Koeleria cristata* and *Stipa comata*. Such areas, usually indicative of a firm soil, are to be regarded as plant societies which for a certain time more or less mask the background of *Andropogon*

scoparius. They are stray pioneer groups of vegetation more especially characteristic of other associations. Later in the season when the onward march of xerophilous conditions has enveloped the hills, *Koeleria* and *Stipa* wane and *Andropogon* pushes rapidly to the maximum and most traces of the former species have completely disappeared. During the late summer *Calamovilfa longifolia* becomes quite dominant in situations where blow sand is still abundant. *Eragrostis trichodes* and *Eriocoma cuspidata* occur at such times near sand-draws or blow-outs where the sand still has a tendency to slide. It is thus seen that, although these species are frequently noted within this association, they are largely "left-overs" from blow-out conditions. They are rather efficient sand binders and hence they serve as convenient intermediary species between *Redfieldia* of the blow-out association and *Andropogon.*

Andropogon hallii is a tall, coarse grass that forms loose, open bunches of a few large stems that are often conspicuous objects in this association. This species is more frequent and abundant toward the tops of hills and ridges especially over the eastern stretches of the sandhills in Holt, Garfield, Wheeler, and Antelope counties. Usually coming to full development later than *A. scoparius* and *Stipa comata,* the tufts of few tall, glaucous stems and broad, blue leaves scattered thinly over slopes and hill tops, are noteworthy features of many hills as the vegetative season approaches its close during the last week of July or the first week of August. The spiny blow-out grass, *Muhlenbergia pungens,* persists for a number of years as small, low, cushion-like mats after the bunch-grass association has become controlling. The hairy grama, *Bouteloua hirsuta,* is also a frequent member of the bunch-grass association in many parts of the hills. The small, low, bunchlike mats four inches or more in diameter occur at widely scattered intervals throughout the region. The sand-enduring, wind-tolerant nature of this species is remarkable.

Two sedges, *Cyperus schweinitzii* and *Carex stenophylla,* are common bunch-grass associates. The former species is characterized by low tufts composed of a few spreading or grasslike divergent stems, thus producing a very open type of the bunch-grass form. These are widely scattered and are interesting because of their extreme xerophilous nature. *Carex stenophylla* on the other hand becomes controlling in certain spots. If one views the hills during the early days of May one is impressed by the appear-

ance in many localities of a greenish tone which contrasts very distinctly with a background of weathered bunch-grasses. This condition occurs long before the appearance of green in the bunch-

Fig. 11. Black grama, *Bouteloua hirsuta*. Plant, showing habit, *a*; flowering spikes, *b*; empty glumes, *c*; perfect and imperfect flowers, *d*; flowering glume, *e*. (From Shantz.)

grasses. Many of the protected pockets often show a very close cover of this species which affords valuable forage. Associated with this sedge other *Carices* are common, especially *C. pennsyl-*

vanica. These *Carex* societies which appear to be closely dependent upon a relatively high soil-moisture relation of the vernal period, persist for about two weeks after which all trace of their presence is soon obliterated with the coming of drier days.

Another grass which sometimes assumes a distinct bunch-grass form in exposed situations is *Panicum virgatum*. However, this species reaches its maximum in the numerous pockets which partly characterize the "choppy hills." Here this grass often covers such more or less protected depressions with a rather close sod. This condition is especially liable to arise if fires are prevented from sweeping such habitats for a number of years. After a few years of unrestricted vegetative development the sandy soil is covered completely with an effective layer of leaf and stem litter and the density of the stand is such that the most of the common interstitials are prevented from entering the areas so controlled. The finely divided refuse from several generations' growth may accumulate to a slight depth over which there is, in the older and more protected "pockets," a secondary tangle of straw and leaves. Refuse of this sort affords a prime starting point for prairie fires. The treatment of accumulated litter must of necessity be handled carefully, especially with reference to the management of plantations of forest trees in the sandhills. At Halsey, Thomas County, where the United States Forest Service is conducting extensive planting operations there is an area of a hundred acres or more that has not been burned over for at least ten years. Many of the numerous "pockets" and "bottoms" that occur within this area show considerable litter which has accumulated from the several generations of *Panicum virgatum* and associated species. These conditions are scattered here and there among the plantations of coniferous trees. The question as to the future management of the plantations must contemplate the reduction of this inflammable material in order to rid the plantations of the possibility of destruction by fire. Perhaps the safest plan would contemplate the pasturage of the area in order that the accumulation of inflammable vegetative refuse may be prevented. Grazing is however attended by dangers which perhaps might become nearly as destructive as fire. Stock might injure to a serious degree the growth of the trees. Then also too severe pasturage is liable to expose the soil of certain slopes to wind action and consequent eradication of portions of the plantation because of this force. An alternative might be found in firing the accumulated

material during calm days. Even under the most advantageous circumstances this method would be extremely risky. The method would be very laborious because of the close spacing of the trees. Furthermore it is frequently the case that the surrounding grasses are taller than the trees so that the more or less hidden trees are very sure to be injured. Because of such relations as these, and because of the ease with which fire escapes, the method must be regarded as questionable. Grazing injury to the young coniferous trees would probably not be great. The solution of the problem is thus seen to lie in the adoption of some grazing rotation.

Aside from *Andropogon scoparius* the most conspicuous plant of the uplands in practically every portion of the region is *Yucca glauca*. This plant follows rather closely the distribution of the dominant species of the bunch-grass association. Because of its evergreen frutescent habit and its great frequency, *Yucca* is one of the most noticeable features of the sandhills. *Yucca* is an especially striking feature of the floral covering during the early days of June when the long racemes or spikes of large whitish flowers may be seen on almost every hill. Typically the species is found over the upper slopes and crests of hills and ridges in the more open sites of the association. Whenever the less conspicuous interstitial species are poorly developed in number and size, *Yucca* assumes a commanding importance.

The *Yucca* appears to thrive in the more open areas of the association. The south and southwest exposures are as a rule the most xerophytic situations throughout the hills. These sites are the typical habitats of this species where it is not only most frequent but also reaches its greatest abundance. Its sand-collecting and sand-holding ability coupled with its extreme xerophilous anatomy makes possible the persistence of the *Yucca* long after all other interstitial species have been tramped out and blown away. It frequently rivals *Andropogon scoparius* in its ability to resist wind erosion and is therefore to be found in numerous places where all of the bunch-grasses and practically everything else have been removed. Fire is the only force of sufficient magnitude, active at present, to eradicate *Yucca*. Conditions where this species is practically the only plant left on the uplands are produced by overgrazing. When such conditions occur over areas where *Yucca* is especially abundant a very striking effect is produced by the dark green rosettes of many swordlike leaves scattered over the otherwise bare sand. Under

these circumstances blow-out rather than bunch-grass conditions prevail. The presence of such species as *Redfieldia flexuosa, Psoralea lanceolata,* and *Muhlenbergia pungens* clearly indicates this relation.

In addition to the species that have been mentioned above there are a number of xerophilous bushes and dwarf shrubs that assume considerable importance in the upland vegetation of various portions of the sandhills. The individuals of such species are sometimes so abundant as to dominate relatively small local areas of this association during certain seasons of the year or sometimes this dominion persists throughout the year. The correlation of these groups with certain physical conditions is not always evident. Chance dissemination accounts for much of the distribution phenomena exhibited by these species although that complex relationship known as competition is very evidently active in a number of cases.

Prunus besseyi is in reality a more abundant member of the bunch-grass association than *Yucca glauca,* but because of its smaller stature and the fact that it is never a very leafy plant the species rarely plays the commanding rôle that is often noticed in the case of *Yucca.* The sand cherry is, however, to be found on almost every hill in nearly all portions of the sandhills. As with the *Yucca,* so this species prefers the more open condition of the bunch-grass association. Such habitats commonly reveal during the first two weeks of May the numerous short twigs of the low, bushy plants with their dense umbels of white or pinkish flowers. At this time other fresh vegetative features are not abundant so that the sand cherry becomes a most welcome and obvious floral element spread over the awakening hills. With the falling of its showy flower parts the sand cherry becomes of less conspicuous nature since the leaf development is not so luxuriant as to attract the eye from a distance. Later in the summer or early autumn when the growth period has closed for most sandhill species, *Prunus besseyi* again becomes especially noticeable because of the many large black fruits that stand out in sharp contrast to the light-colored sand below. Unfortunately a species of *Exoascus* sometimes completely destroys all of the fruits of the sand cherry. The sand cherry never assumes sufficient dominance to rival the bunch-grasses, being as a rule merely an important principal species.

Another characteristic shrub is *Ceanothus ovatus* which becomes especially abundant in the central and southern portions of

the region. A variety, *C. ovatus pubescens*, is more common in the sandhills than the glabrous form. This low brush with pubescent leaves and petioles occurs in characteristic tangles of fine woody stems about two feet in height. The individual plants become much branched and very bushy so that during midsummer when they are in full leaf they present a conspicuous appearance. The typical growth habits of the plant result in the development of such low bushy patches which vary from 3 to 30 feet in diameter with an approximately circular outline. The smaller-sized patches are more plentiful and typical. Such patches frequently occur as a conspicuous modification of the bunch-grass association over large areas. Sometimes very regular colonies with a uniform diameter of about one and one-half yards and nearly equal intervals greatly change the typical appearance of the association. Many of the highest hills south of the Dismal River in Thomas and Logan counties are dominated by this species. The density of the plants, especially in the larger colonies, often becomes so great that few species invade such areas. Consequently when the leaves have fallen from the plants in a local area controlled by *Ceanothus* a peculiar barrenness becomes prominent.

Rosa arkansana assumes a position of importance in this association in various parts of the region. Over the less exposed slopes the wild rose becomes aggregated into dense brush. The low tangle of flexible, thorny stems is often controlling in patches several acres in extent over the uplands. Societies of this nature are especially noteworthy constituents of the early aestival period when thousands of large showy blossoms charge the atmosphere with delicate perfume. These patches occur in such dense stand as to resist invasion by bunch-grasses and bunch-grass interstitials to a high degree. The species can not endure serious movements of the surface soil and is slow to recover after being buried by the sand so that it is not often found in abundance in exposed situations. Even in protected situations, as on the lee slopes of hills with active blow-outs, the rose soon gives way before the encroaching sand and quite early yields up its habitat to species better fitted to endure and finally to conquer these conditions.

Toward the southwestern limits of the sandhill region *Artemisia filifolia* becomes very abundant as a member of this association. This sagebrush covers many acres of land, somewhat harder than typical bunch-grass land, with its characteristic gray bushlike

plants so well described by Pound and Clements under the "Artemisia filifolia Formation."

Still another common prairie shrub, *Amorpha canescens,* is noted at many stations in the sandhills. The dominion of this species is also local and so partakes of the general effects produced by the same plant in other portions of the prairie-grass formation. The prairie shoestring, as it is commonly called, is characteristic of firm soils. With *Kuhnistera villosa* this species forms extensive societies of low bush in the harder soils north of the Niobrara River. Within the heart of the sandhills it occasionally assumes a dominant rôle over small local areas. The low, finely branched plants with a dense cover of silvery leaflets always stand out as very prominent objects of the prairie flora. This species as it occurs in the sandhills seldom becomes so socially exclusive as do *Rosa* and *Ceanothus.*

The open nature of the bunch-grass association is a condition which makes possible the presence of a great many secondary species. The most common of these widely distributed interstitials have been enumerated in the list of secondary species of the association. Besides the above woody species that are of common occurrence in more or less density as characteristic societies, the following species have a wide distribution and frequently occur as closely aggregated patches or societies: *Lygodesmia juncea, Lathyrus ornatus incanus, Psoralea lanceolata, Anemone caroliniana, Helianthus petiolaris, H. subrhomboideus, Lesquerella argentea, Froelichia floridana,* and *Eriogonum annuum.* Certain of these species are notably seasonal in their appearance and for short periods they are conspicuous, locally dominant species of the association. Thus *Lathyrus ornatus* is a distinctive species of very sandy hilltops and ridges where in late spring or early summer it fairly covers the ground with a prostrate tangle of slender vinelike stems and tendrils. This plant is a profuse bloomer and when at the height of its flowering period is one of the most delicate and beautiful species of the whole state. *Froelichia floridana* and *Eriogonum annuum* usually occur singly or in loose patches scattered among the bunch-grasses, but occasionally dense communities of these are seen. The latter is especially common on valley floors and bottoms of pockets where the soil is quite firm.

THE MUHLENBERGIA ASSOCIATION

This association occupies upland habitats similar in topography

and general edaphic conditions to those of the bunch-grass association. The most perfect degree of development and the greatest area of the Muhlenbergia association at present are to be found over the uplands of central Garden County and western McPherson County. However, the association has been seen in various other portions of the sandhills where the extreme severity of certain ecological factors has brought it into existence. Within the above center this association dominated by *Muhlenbergia pungens* occupies hundreds of acres of the uplands from which *Andropogon scoparius* and many of its numerous associates are all but completely excluded.

COMPOSITION OF THE MUHLENBERGIA ASSOCIATION

DOMINANT SPECIES

Muhlenbergia pungens

PRINCIPAL SPECIES

Bouteloua hirsuta	*Prunus besseyi*
Lathyrus ornatus incanus	*Psoralea lanceolata*
Phaca longifolia	*Yucca glauca*

SECONDARY SPECIES

Allionia linearis	*Opuntia humifusa*
Andropogon hallii	*Rosa arkansana*
Andropogon scoparius	*Senecio plattensis*
Calamovilfa longifolia	*Stipa comata*
Lygodesmia juncea	

The Muhlenbergia association is very commonly found as scattered relict patches about blow-outs and sand-draws. This is the case especially in those places where the latter association has been seriously impaired by fire or continued overpasturing. In fact we shall see that *Muhlenbergia pungens* is one of the regular members of the blow-out association. Whenever blow-out conditions are brought to bear over extensive upland tracts by either of the above agencies, blow-outs are regularly generated in the most exposed situations. These expanses of overgrazed land are furthermore characterized by much surface which is not directly exposed to the extreme erosion which results in the formation of blow-outs or sand-draws. Yet such broad, sloping areas are often so open, dry, and wind-swept that the bunch-grasses are slow in invading, and accordingly they may be controlled by an altogether different type of

vegetation from that of the bunch-grass association and sufficiently different from the blow-out association to be worthy of separate classification and treatment. Successionally the Muhlenbergia association is very evidently intermediate between these two upland associations but with a closer relationship to the blow-out association. There is much evidence in addition to that cited above that this association preceded the bunch-grasses during the initial invasions that marked the early population of the sandhill region by plants. Furthermore it appears that when overgrazing or other causes have reduced the bunch-grass association to a very low degree the two types of vegetation which then make their appearance are the blow-out association and the Muhlenbergia association. I have found wherever this association is most highly developed that overgrazing or repeated firing or both have been the forces that have probably made possible its origin. In such places, then, we naturally find the maximum expression of the association where it occupies the less severe or slightly more stable uplands surrounding points of greatest exposure whereupon typical blow-outs are developed with the physical and vegetative features to be noted elsewhere in this paper.

Some idea of the peculiar typical appearance of this association may be obtained from a brief description of the dominant species. *Muhlenbergia pungens* is a low grass characterized by tufted stems with very glaucous and extremely rigid, narrow, involute-setaceous leaves from three to five inches in length. These leaves are arranged in two ranks upon the short erect culms, which arise from creeping rootstocks, and which are inclined to be grouped into small tufts or cushions that always lie close to the sand. The decumbent bases of the culms bring the plants down to a height of less than four inches. These low irregular clusters a few inches in diameter closely crowded together present a remarkable spiny, carpet-like cover wherever the species is controlling. This growth relation is frequently so emphatic as to exclude nearly all other species from areas often many square yards in extent. From a distance such areas might be mistaken for short-grass land covered with a carpet of *Bouteloua* if the very sandy substratum was not evident. *Muhlenbergia pungens* is an excellent sand-collector. The rhizome type of propagation and dissemination is so well developed that the plants recover very rapidly from sand burial and are thereby enabled to maintain a foothold against active sand movement. We have here

one of the most effective sand-binding, sand-collecting, or dune-forming species of the region. The dune-forming relation is most often seen upon the more exposed slopes and within large shallow blow-outs. The peculiar ability of this species enables it to grow into the light when buried by the sand. Thus as the radial distribution of the colonies is increased the plants are also raised somewhat above the level occupied before the last sand collection. The combination of these two directions of growth maintains a constant obstacle in the face of the wind and because especially of height increment and continued sand collection the small or embryonic dune increases in height. Cowles (30) has described the similar dune-forming ability of *Ammophila arundinacea* in tracing the life-history of an *Ammophila* dune on the shore of Lake Michigan. The equipment of xerophytic adaptations is perhaps even more perfect in *Muhlenbergia pungens* than is the case with *Ammophila arundinacea.* The former species within the region under study apparently swings from the dune-forming habit to the broad carpet-forming nature according as the exposure is greater or less severe. Both tendencies are abundantly represented in that portion of the sandhills already noted wherein this association is seen in its most typical and widespread expression. After midsummer when nearly every glaucous plant of *Muhlenbergia* is provided with a narrow brushlike panicle of bright reddish-purple or rose-colored spikelets the areas or patches, or embryonic-dunes, controlled by this species become veritable blazes of color.

We have already seen that *Yucca glauca* is one of the typical widespread principal species of the bunch-grass association. This species is even more pronounced in the Muhlenbergia association. The *Muhlenbergia-Yucca* combination is much more successful in the face of extreme dune conditions than is *Andropogon-Yucca.* The soap-weed appears always to enter such wind-swept areas long before the bunch-grasses and to leave after they are gone. Within the *Muhlenbergia* maximum the highest hills are frequently studded with the *Yucca* hosts whose dark individuals and segregated rosettes stand out in vivid contrast against the glaucous background of *Muhlenbergia pungens* or bare sand. It is here that *Yucca* often exercises an important rôle in holding the uplands against the fury of the wind and sand-blast. I have often seen hilltops and ridges firmly resisting destruction because of the presence of myriads of *Yucca* plants. Sometimes a knoll with a great many of these

plants localized towards the crest becomes excessively eroded on the flanks in such a manner that the surrounding sand with its open vegetation is blown away to considerable depth bordering the sand volume actually penetrated and held in position by the roots of the *Yuccas*. Columns or cylinders are thus produced that vary from 10 to 30 feet in diameter and from 6 to 10 feet in height. These may resist for a long time the destructive agencies raging about them. The wind sometimes succeeds in tearing its way into these columns and then the long, brown, thick woody roots become exposed. If such action is continued the columns become thoroughly undermined and many of the plants fall outward and are blown away. A more vivid picture of the severity of the action of the wind can not be seen anywhere in the state than here where one of the *Yucca* columns has been torn and twisted until many of the plants lie upon the bright sand, a tangled mass of large, dark brown roots crowned with the green rosettes of dagger-like leaves.

The presence of societies of *Prunus besseyi* only within protected areas of this association shows in a convincing manner the degree of wind-avoidance typically possessed by this species. In the bunch-grass association this species is found upon hilltops and ridges under all exposures but there the necessary protection from the full fury of the wind is afforded by the bunch-grasses. The even more wind-sensitive species, *Ceanothus ovatus,* was not found at a single station in the Muhlenbergia association.

Further notable structural characteristics of this association are seen in the number and abundance of the principal and secondary species. The few interstitials are especially contrasted to the condition already described for the bunch-grass association. All of these species are either very wind-tolerant or they occur only upon protected slopes within this association. The latter is especially true for *Prunus besseyi, Bouteloua hirsuta, Rosa arkansana, Senecio plattensis,* and *Lathyrus ornatus.* The extensive and efficient rhizome systems of *Phaca longifolia, Psoralea lanceolata,* and the naked, extremely xerophilous nature of *Lygodesmia juncea* are characters that enable these species to assume an importance here that is seldom seen elsewhere. The painted-pod, *Phaca longifolia,* for instance, reaches a frequency and an abundance in this association that is second only to its distribution in the blow-out association. The presence of *Calamovilfa longifolia, Andropogon scoparius,* and

A. hallii may be more or less common and may be of either relict or invading nature.

Occasionally other typical upland plants make their appearance in this association as secondary species but the typical nature of the association is expressed in the dominion of *Muhlenbergia pungens* with the presence of relatively few associates. When the principal and secondary species increase notably in frequency and abundance, the association rapidly approaches the more extensive bunch-grass association.

THE BLOW-OUT ASSOCIATION

The most striking and peculiar habitats of the uplands in the sandhills of Nebraska are the blow-outs. The present blow-outs appear to be the remnants of a condition that was probably general and much more extreme over the whole region hundreds of years ago when the first plants began to migrate into the region. These blow-outs are quite different in form and ecological relation from those that occur in other parts of the world, Cowles (30), Gleason (37), Cockayne (26). Our blow-outs are rounded or more commonly irregularly conical depressions of varying depth and diameter, formed by the blowing of the sand and vegetation from certain areas on the upper slopes and crests of the hills and ridges. The more or less conical depression is sometimes almost circular in outline. An irregular form is, however, more common both as to the perimeter of the top and the configuration of the inner slopes. One side of the rim is usually considerably lower than the opposite side because of the slope of the hill or ridge within which the blow-out has been formed. Landslides, the presence of stratified sands, the coalescence of neighboring blow-outs, and the encroachment of vegetation are factors that frequently unite in the production of bizarre forms characteristic of the rim and inner surfaces of blow-outs.

The size and depth of blow-outs vary with the position and the age of the depression. In the beginning blow-outs cover a few square yards and are but a few inches in depth, but in the extreme cases they become hollowed out to a depth probably exceeding 100 feet while the greatest circumference may be more than 600 feet. I am fully aware of the presence of *plane* sand-sweeps that are much broader than this and of sand-draws sometimes more than a mile long, but these should not be confused with typical blow-outs. The term blow-out should be restricted to the crater-form depres-

sions which are so numerous in certain parts of the hills and which really exhibit the *unique* blow-sand conditions of the region. This association includes the "Blow-out Formation" and the "Sand-draw Formation" of Pound and Clements.

Since the prevailing winds of the region are westerly and since the blow-outs are the direct products of wind action, these peculiar land forms are mostly confined to the western sides of the hills and ridges. Blow-outs usually occur below the summit of the hill but occasionally one finds a case where the whole top of a hill or ridge has been blown away and the position is then occupied by an enormous blow-out. The greatest number and usually also the largest blow-outs occur upon the northwest exposures, but blow-outs range from this position to the southwest exposures. The position depends somewhat upon the shape of the particular hill in question as well as its relation to the neighboring hills which may deflect the wind currents toward a certain slope or crest. A single hill sometimes shows only one blow-out although this one may be so large that the whole side or top of the hill is occupied. Frequently several blow-outs originate upon a single hill or ridge and these may coalesce rather early so that a single large crater is formed which possesses several secondary depressions.

The almost complete restriction of blow-outs to the westerly slopes of the uplands results in the production of very different appearing landscapes according as to whether you face eastward or westward. Facing eastward you look directly into the many circular or crescent-shaped craters with always much bare sand exposed over their inner slopes. These alternate in varying proportions with hills without blow-outs which naturally show one of the other upland plant associations. As you face westward the blow-outs are never so conspicuous since you view the opposite sides of the hills and even when blow-outs are seen in this view it is their highest or eastern rim that one sees and as a consequence the depression is not visible. In the case of some of the larger more active blow-outs, when such sand is being hurled out of the depths and scattered upon the lee slope of the hill or ridge, blow-out conditions are quite readily appreciated even as one looks westward. These areas of comparatively bare sand upon east-facing slopes are not common however and when present they serve to break up the remarkable continuity of the bunch-grass landscape.

Blow-outs do not occur upon all hills. Even in those portions

of the region which reveal the greatest numbers of such depressions there are extensive stretches of the hills covered so effectively with vegetation that blow-outs are seldom seen. The unmistakable evidences of former wind action are, however, present in abundance in such areas. The most universal indices of former conditions are seen in the configuration of the hills and ridges and in the presence of blow-out relicts.

Regions of present maximum blow-out conditions are found between the Middle Loup and Dismal rivers in Thomas and Hooker counties, and in the lake district above the headwaters of Blue Creek in Garden County. In certain places the ranges of hills are little else than ranges of blow-outs of various ages. At one place near the Dismal River I counted sixty-eight blow-outs within an area of approximately one square mile. These were large active blow-outs ranging in size from 20 to 75 feet deep and from 35 to 150 feet in diameter. In addition to this number there were many smaller embryonic blow-outs in this same area, and still others that had reached a late stage in vegetative stabilization. On the other hand there are hundreds of square miles, as in Cherry and Holt counties, that show few or no blow-outs. Even in such comparatively blow-out-less areas, however, one occasionally finds enormous blow-outs upon the highest hills or ridges in the neighborhood.

Composition of the Blow-Out Association

DOMINANT SPECIES

Calamovilfa longifolia
Psoralea lanceolata
Redfieldia flexuosa

PRINCIPAL SPECIES

Cristatella jamesii
Eragrostis trichodes
Eriocoma cuspidata
Muhlenbergia pungens
Pentstemon haydeni
Phaca longifolia
Polanisia trachysperma

SECONDARY SPECIES (invaders)

Anogra cinerea
Asclepias arenaria
Chrysopsis villosa
Cyperus schweinitzii
Eriogonum annuum
Euphorbia petaloidea
Froelichia floridana
Hymenopappus filifolius
Lathyrus ornatus incanus
Lygodesmia juncea
Meriolix serrulata
Prunus besseyi
Rumex venosus
Sideranthus spinulosus

Sieglingia purpurea *Tradescantia occidentalis*
Stipa comata

Blow-outs originate on an exposed upper slope when the cover becomes broken or seriously depleted from any cause. As the wind sweeps up and over such slopes it rolls the heavier sand grains along on the ground but catches up the finer particles and carries them over the crest of the hill a few yards farther away and may drop them upon the leeward face of the hill. As more and more sand is carried away in this manner and the uprooted plants are swept on with the gale the embryonic blow-out comes into existence. During these early stages the blow-out appears as an area of bare sand a few feet or yards across and a few inches in depth over which the wind sweeps and continues to eat its way downward. The roots of deeper-rooted species are exposed and soon the whole plant is blown away. At this time the woody root-remnants of certain perennial bunch-grass associates frequently appear strewn over the surface of the depressions which may now be hollowed out to a depth of 20 to 40 inches. The dead roots become stripped of their cortical tissues. Finally the wind eats its way far beneath the point of penetration of the deepest-rooted species (except possibly *Yucca)* and all these are then added to the accumulating débris on the lee slope or elsewhere.

The two principal factors that enable the wind to begin this work of destruction are fires and overgrazing. Either factor may result in reducing the plant cover to a point below effective wind resistance and, as soon as this occurs, destructive wind erosion is sure to begin upon exposed slopes. Nothing is quite so effective as a prairie fire in clearing the vegetation and exposing the soil to wind action. A severe fire or repeated burning destroys absolutely everything above the surface of the ground in so far as the plant cover is concerned. The old practice of burning the range to increase and improve the yield of forage has practically ceased since the great majority of stockmen and homesteaders have learned the folly of such a method. A recently burned range is a truly beautiful sight in early summer when the wealth of new growth appears with all its freshness, often in sufficient quantity to mask the charred surface. This freshness is especially notable in such places because it is not at all diminished by the presence of old stems, leaves, and other litter of bygone generations of plants. The perennial roots of *Andropo-*

gon, for instance, which are seldom killed except by the most severe fires send up a number of green stems and leaves whose presence is made much more emphatic because the old stems and leaves have been consumed by the fire. However, when the high desiccating winds of August reach such areas the unprotected growth often suffers very seriously and is often unable to withstand the fury of the wind and the cutting sand-blast.

Grazing animals often greatly reduce the plant cover of the uplands and the soil may be tramped bare of plants for wide intervals so that the wind readily strikes at the open sand and thereafter range destruction may be rapid. It must not be supposed that the bunch-grasses will soon be followed by some more valuable species, such as blue grass, as Gleason (37) reports for the inland dunes of Illinois.

When the young blow-out is no more than one foot in depth the sand begins to slide into the depression from the sides. This sand which rolls into portions of the shallow blowout is caught up by the wind and blown away. Sand continues to slide in with the increasing depth of the blow-out and in this way the depression increases in area at the same time that the wind is scooping it out to a greater depth. These two processes continue for a number of years with varying rate for different exposures until, as in many cases, the highly developed crater-form depression is blown out of the hill. Naturally with the increasing depth of the blow-out the direct force of the wind becomes considerably checked as it strikes upon the prominent inner face of the blow-out and is partially deflected downward. As the wind impinges upon the farther inner slope of the blow-out, which soon assumes a gradient of about 30°, a prominent reverse current is developed which strikes beneath the rim and dips more or less into the bottom of the deepening crater. In this manner wind action reaches to the very bottom of the blow-out which at this time may be fifty or more feet below the highest point of the rim. The grinding action of these downwardly deflected currents heavily laden with finely divided quartz particles can best be appreciated by placing oneself in such an intensely dynamic habitat on an especially windy day. These winds continue to loosen sand at the sides of the blow-out, causing it to slide into lower depths only to be caught by the wind and hurled over the rim and deposited upon the advancing lee slope. Because of the presence of grinding spiral winds in deep blow-outs during this rather late period of

blow-out development, I have spoken (53) of this as the action of a "sand mill."

After many years of this sort of growth blow-outs at the end of their maximum activity become depressions varying in size and form as has already been indicated. The inner slope which faces the wind is always the longest and most extensive side of the interior. The gradient of this slope is usually about 30°, although this angle varies somewhat in different blow-outs according to the degree of compactness of the sand. The opposite or lower side of the blow-out is usually much steeper, often being nearly perpendicular in places. This condition is due to the fact that the sand continually rolls from this side and is blown out over the opposite side while the side toward the wind is never exposed directly to wind action. The deflected currents aid in undermining this margin and so land-slips are very common on this side of the blow-out but the slope remains comparatively steep unless indeed the bottom of the blow-out occurs on a level with the slope of the hill when the conical form becomes less prominent. Very commonly under these conditions the lateral sides of the depression are much steeper than the wind-swept slope.

The lee slope of a hill with an active blow-out often becomes much steeper than any other exposure because of the influence of sand-collecting plants which become established in such places. These, usually grasses, keep above the accumulating sand deposits by means of a combined horizontal and vertical growth and at the same time hold the sand at a steeper gradient than it would assume in the absence of the sand-collectors. Such slopes often become as steep as 60°.

Blow-outs were found in Garden County in rather low hills near the lakes from which the sand had been removed until the saturated zone was reached. The bottoms of such blow-outs were covered by a few inches of clear water and in a single case I found *Lemna minor* and a species of *Potamogeton* in such a place. The same "blow-out pond" was furthermore interesting because of the presence of a thin marginal belt of *Eleocharis acicularis* and *Cyperus inflexus*. At the time I saw this blow-out the sand was encroaching upon the depression from a neighboring blow-out and it appeared that in a few years this area in which pond-weeds and blow-out grasses were so closely associated would be completely covered by sand.

The combined action of desiccating winds of high velocity, great extremes of air and soil temperature, excessive transpiration, and the unstable soil of the active blow-out is a condition that few plants can endure. Consequently from the period of early youth, and continuing throughout the years of greatest blow-out activity, plants fail absolutely to gain a lasting foothold within these depressions. Sooner or later, however, the blow-out reaches a period that may properly be termed *maturity*. At this time a depth has been reached such that even the most vigorous wind action fails to increase it further, the sand mill becomes ineffective, and the sand that slides into the bottom of the blow-out tends to remain there. In some cases, especially during quiet periods in early spring or during wet seasons, landslides reach the bottom of the depression and at such times a much less agitated condition makes possible the germination of numerous seeds that have been carried into the depths. If the relatively quiet conditions persist for many days some of the more wind-tolerant species become established and are enabled to resist the returning activities of the wind. Henceforth the extreme physical conditions wane and the sparse plant cover, gradually creeping upward, slowly becomes the master of the situation. Old age, or the period of blow-out decadence, is traced from this time in the development of the vegetation from these first successfully established centers until the whole crater-like depression is claimed, first by the pioneers of the blow-out association, but ultimately by the bunch-grasses and their common interstitial species.

The position most commonly captured by the first invaders usually lies far down upon the slope of the blow-out. Quite frequently the first plants to become established are found over the very lowest points of the depression. Points of establishment are sometimes seen higher on the inner slopes. These are commonly made possible by the sliding in of bunch-grasses which then present a relatively stable point about which blow-out pioneers may become established. Tufts of *Andropogon scoparius* and of *A. hallii* have often been seen far down upon the slopes, having been carried there in a slide that followed a heavy rain. These resistant spots are frequently centers of growth and they usually lead to a more certain and rapid reclamation of the bare slopes.

The first plants to become established at this stage in the life of the blow-out are certain grasses and legumes. The pioneer grasses are known as "blow-out grasses." The most important of these is

Redfieldia flexuosa which has been accorded the honor of being the very first pioneer in the reclamation of these sandy craters. *Redfieldia* may be the only plant in such places for many years, although as a rule other early invaders, notably the leguminous species, *Psoralea lanceolata* and *Phaca longifolia,* are to be found occupying the same situations. Seedlings of numerous species have been found in blow-outs in early spring. During the resting period the disseminules of many species are blown into the deeper blow-outs and may lodge there more or less permanently. With the resumption of growing conditions in the spring many seeds germinate in these spots and at such time the bottom of the blow-outs may be covered with a veritable green sward composed of seedlings, most of which however disappear before reaching much size because of the approach of desiccating winds accompanied by the usual sand movements. Seedlings of *Psoralea lanceolata* and *Cristatella jamesii* are especially abundant at such times. Only the seedlings of the most hardy pioneers are permanently enabled to resist the fury of the approaching summer conditions, but these serve as effective centers of propagation from which the vegetative wave finally sweeps over the entire blow-out.

I have seen numerous blow-outs in which the initial steps in the development of the blow-out association were taken by *Psoralea lanceolata.* However, in the most of the vast number of blow-outs within the region *Redfieldia flexuosa* is the most abundant and controlling species of blow-out pioneers. Hundreds of blow-outs occur in which this is the only plant present. Still other grasses, notably *Muhlenbergia pungens* and *Eriocoma cuspidata* toward the western portion of the region, and *Calamovilfa longifolia* and *Eragrostis trichodes* throughout, are of less importance during the initial processes that eventually culminate in the stabilization of the blow-out. Pound and Clements report (57) that *Calamovilfa longifolia* is regularly substituted for *Redfieldia* and *Muhlenbergia* in certain localities of Antelope County. All these species are effective sand-binders and, after *Redfieldia* or *Psoralea* has paved the way, they aid greatly in the fixation of the substratum and in this manner facilitate the establishment of numerous secondary species that follow in the wake of the pioneers.

The early phenomena in connection with the decadence of a blow-out cover an interval of several years. For a number of years after invasion *Redfieldia* extends its area by slowly pushing its

slender rhizomes through the sand and firmly binding the open soil with its radially spreading network of wiry rhizomes and fine roots. Sometimes *Psoralea lanceolata* is a companion in this early work and with its similar type of propagation this species aids materially in

Fig. 12. Blow-out grass, *Redfieldia flexuosa*, showing habit and details. An erect stem, *a*; rhizome, *b*; spikelet, *c*; single lemma and palea showing fringe of hairs, *d*. Criginal.

the fixation of unstable sands. The wirelike rhizomes of *Redfieldia* are usually encountered at a depth of from 4 to 12 inches. Naturally this varies somewhat with reference to wind action since during a number of days of high wind the rhizomes may actually be uncovered in certain more exposed spots in the blow-out. From these rhizomes,

which are normally distributed in the form of a close network with many fine rootlets spreading throughout the meshes, there arise few-leaved tufts of long, narrow, flexuous leaves. This species can endure longer periods of severe wind-whipping than any other similar plant of the region. The rhizome method of propagation and the ability to recover after being buried or uprooted are noteworthy characteristics possessed by the common blow-out pioneers. Especially are these phenomena characteristic of, and most highly developed in, *Redfieldia flexuosa, Psoralea lanceolata, Muhlenbergia pungens,* and *Calamovilfa longifolia.*

The time required for the complete fixation of the sandy soil of a blow-out through the agency of invading plants has never been determined. Studies have been begun which should in the course of years throw some light upon this question. Permanent quadrats have been established within certain blow-outs and careful complete lists of species and individual plants have been made for the same three large, comparatively young blow-outs in the hope that some data may be collected bearing upon the time that elapses between the first successful establishment of vegetation within a blow-out and the final (or semifinal) occupation of the same areas by the bunch-grass association.

As the tufts or erect offshoots of the pioneer species increase in number with the spreading of the hypogean stems, the soil becomes much more stable and conditions gradually arise that make it possible for the incoming and establishment of certain principal and secondary species although the plant cover may still be very sparse. These later arrivals are not numerous but are fairly constant. *Eragrostis trichodes, Eriocoma cuspidata, Pentstemon haydeni,* and *Polanisia trachysperma* are the more common and typical species that become a part of the blow-out association at about this time. The latter species with *Cristatella jamesii* are regular pioneers in sand-draws as will be noted again in the following pages. In addition to these plants, which with the dominant species may be regarded as the most characteristic and frequent members of the blow-out association, there are numbers of the regular members of the bunch-grass association that come into the blow-out. The coming of these species usually indicates a considerable degree of stability already attained within the blow-out and is prophetic of the ultimate establishment of the bunch-grass association in the regular normal progress of succession. The more common and abundant

species of this nature are indicated in the list of secondary species of this association upon an earlier page. The structure of the association at this time resembles somewhat the "sand-hills mixed association" of Shantz (60), especially when, as frequently happens, *Calamovilfa longifolia* is present in considerable abundance.

Fig. 13. Sand-grass, *Calamovilfa longifolia*. Clump, showing habit, *a*; single plant, *b*; spikelet, *c*; spikelet with empty glumes removed, *d*. (From Shantz.)

With the invasion and multiplication of these forms the blow-out becomes in the course of years completely covered. In this manner blow-out conditions finally become far removed and the bunch-grasses with many of their common associates that have been kept out for so long a time now take possession of the areas so well prepared by the members of the blow-out association. The disap-

pearance of the pioneers, already far advanced, is soon completed and the transformation from blow-out association to bunch-grass association becomes perfected. Certain of the pioneers linger for a time as relicts in the more sandy areas between the bunch-grasses upon the most exposed sites.

With the development of the bunch-grasses and their numerous interstitial species all traces of the blow-out association ultimately disappear from large areas of the uplands. The change from the one association to the other is often so complete that the only indications of the former history of the habitat are seen in the crater-form depression which persists with its acquired grassy covering.

Frequently various stages in the movement of this floral wave that sweeps over the blow-out may be seen in a single blow-out. These stages are especially noticeable when the original point of colonization lies near the lowest point in the blow-out. From this starting point the succession moves up and over the inner face until the upper rim is reached.

Next to blow-outs, the sand-draws present the most crucial physical environment to be found within the region. The sand-draw may even become more severe than the blow-out because of the rushing torrents that occasionally pour through these drainage lines. Sand-draws as a rule are somewhat like dry stream beds. The course of the draw is usually irregular; the head of the draw may be far back in the hills and the course may continue for a mile or more as a regular, rather steep linear depression. As the draw leads farther away from its point of origin the gradient becomes less and as a rule the bottom wider. Such draws vary in length from a few hundred yards to several miles and in width from 10 to 45 feet or more. The flanks are usually steep and inclined to slip. The general form of the draw is that of a trough with a relatively flat bottom. The floor of such draws is covered with gravel or coarse sand several inches in thickness. The texture of the soil varies considerably at different places in the same draw because of the influence of wind and water in sorting the particles.

Sand-draws are few in number in our sandhills as compared with blow-outs. Such habitats are found in greatest number and in best development toward the extreme southwestern border of the main sandhill region in Deuel, Garden, Cheyenne, and Morrill counties where the largest draws lead from the sandhills toward the North Platte River.

The effects of wind erosion are pronounced in sand-draws during the more droughty seasons. The level of the floor is shifted by such a force as well as by water after sudden thunderstorms. The combination of wind and water erosion results in the production of a sand-draw floor of remarkable instability which offers a precarious foothold for plants. Species that are successfully to populate sand-draws must resist conditions imposed by flood waters in addition to those of a wind-shifted substratum. The slipping or sliding flanks of the draw present conditions somewhat similar to those already described for certain portions of blow-outs. On the whole, then, it is seen that the life conditions in sand-draws are somewhat like those of blow-outs, but there are additional rigors imposed by conditions usually absent in the more common blow-out depressions. These serve to differentiate quite clearly sand-draws from blow-outs.

The plants that first invade sand-draws are *not,* as a rule, grasses or legumes with a highly specialized rhizome mechanism as we have seen for blow-out pioneers. As stated by Pound and Clements (57): "The regular and habitual inhabitants of these situations are but two, the closely related *Polanisia trachysperma* and *Cristatella jamesii.* These two species which appear very much alike are almost entirely confined to such areas, and when found elsewhere are in sandy situations of the same essential character. They constitute the bulk of what little vegetation there is in the sliding sand on the sides of dry canyons in the sandhill region and in sand-draws." This statement must now be somewhat modified since a number of sand-draws have been seen with many additional species and some such areas which contained the usual blow-out pioneers. Indeed the latter species are sometimes controlling in sand-draws as in blow-outs. Near the lakes in Garden County, for instance, there are many very large active sand-draws that are practically free from vegetation save small patches here and there of *Cristatella* and *Polanisia.* There are other sand-draws within the same area, however, that show different or additional phases of the sand-draw succession. Some such draws are controlled by *Psoralea lanceolata* and others by *Redfieldia flexuosa.* Others show various mixtures of these two regular blow-out pioneers, and indeed mixtures of these two species with *Cristatella* and *Polanisia* were found in a number of places. These observations, made under the typical sand-draw conditions as first described by Pound and Clements,

serve to modify the older ideas in regard to "sand-draw formation" and to place the sand-draw perhaps somewhat nearer its true relationship with the rest of sandhill uplands.

Polanisia and *Cristatella* are both annuals and hence have little or no direct influence in the production of ultimate stability over the dynamic sand-draw floor. If left to the capers alone, sand-draws would probably always retain their extreme dynamism. However, these plants aid in an indirect manner in facilitating vegetative encroachment by presenting local spots of relatively quiet sand within which one or another of the perennial sand-holders may become established. The presence of seedlings of *Psoralea lanceolata* in early spring near similar rather slight obstacles indicates that the sometimes persistent patches of the two capers might serve as foci for the establishment of sand-binding species.

A certain degree of stability produced by these early invaders makes possible the invasion of sand-draws by numerous secondary species that migrate from neighboring associations. As a result of this activity the sand-draw begins to lose its emphatically nude character and to assume a vegetative cover resembling the bunch-grass association. The more common species that share in this earlier invasion after the regular blow-out pioneers and *Cristatella* and *Polanisia* have prepared the way are: *Munroa squarrosa, Meriolix serrulata, Sieglingia purpurea, Euphorbia petaloidea, E. geyeri, Ipomoea leptophylla, Collomia linearis, Chrysopsis villosa, Argemone intermedia,* and a number of ruderal species such as those of *Gaertneria, Ambrosia,* and *Artemisia.*

The fixation of the sand-draw may proceed from both ends. At the upper extremity the culminating type is that of the bunch-grass association, while below various ruderal species appear to hold the ground for a much longer period, probably because of the presence of considerable silt and a higher water content at such places. The encroachment also commonly progresses from the sides of the draw. Ultimately these irregular belts more or less completely cover the depression and for the greater portion of its length the sand-draw becomes completely merged with the bunch-grass association.

The discovery of these additional life-history relations leads to the conclusion that the "sand-draw formation" of Pound and Clements, at least as it occurs within the sandhill region, is but a peculiar modification or variation of the blow-out association as described in this paper. Accordingly sand-draws are destined to become assimi-

lated with the bunch-grass association, the chief association of the prairie-grass formation as it occurs over the Nebraska sandhills.

THE SPEAR-GRASS ASSOCIATION

This association is one of the minor sandhills associations. In its most clearly defined condition it is well represented in the "Stipa Formation" of Pound and Clements (57) which reaches its highest degree of development north and west of the sandhills. The association is therefore an eastern modification of the "Grass Formation of the High Prairies" of the Phytogeography of Nebraska which is met at frequent intervals in the western, northern, and eastern portions of the sandhills region. It is also found as isolated patches in dry valleys and upon stable hills in all parts of the region. In the latter form this association is broken up to such a degree that it frequently appears as a locally dominant type within the bunch-grass association.

The tendency toward the development of a more open association, somewhat simulating the bunch-grass condition, is the commonest expression of this association as it is found in the sand-hills as contrasted with the more distinctly sod-forming habit that Pound and Clements (57) noted farther westward.

Developmentally the spear-grass association is to be regarded as a later stage than the bunch-grass association of the sandier uplands. This stage may pave the way by still further accumulation of litter and humus for the later occupation of the hills by the short-grass formation toward the west, or toward the east the final stage may be one of the more distinctly sodded associations of the prairie-grass formation. This intermediate position is very evident in many localities.

The dominant species of the spear-grass association is *Stipa comata.* This western *Stipa,* with *Koeleria cristata* as a common associate, is controlling in many parts of the hills where wind action has been more or less conquered and where the bunch-grass association has been completely displaced over many square miles of rolling hills. The lessened wind action is shown by the relative scarcity of blow-outs. As a rule the substratum of this association is less sandy and contains more organic matter than that of the bunch-grass association. *Andropogon scoparius* and *A. hallii* are occasionally seen as relicts in the more sandy portions and along the borders of this association.

Composition of the Spear-Grass Association

DOMINANT SPECIES

Stipa comata	*Koeleria cristata*

PRINCIPAL OR SECONDARY SPECIES

Abronia fragrans	*Erysimum asperimum*
Allionia linearis	*Lacinaria punctata*
Amorpha canescens	*Lupinus plattensis*
Andropogon hallii	*Malvastrum coccineum*
Andropogon scoparius	*Monarda citriodora*
Anogra coronopifolia	*Pentstemon albidus*
Aragallus lamberti	*Plantago purshii*
Aristida purpurea	*Psoralea argophylla*
Aster canescens	*Psoralea digitata*
Astragalus adsurgens	*Psoralea esculenta*
Astragalus crassicarpus	*Psoralea tenuiflora*
Astragalus mollissimus	*Stipa spartea*
Cactus viviparus	

Large areas of sandy hills bearing this sort of vegetation are to be found at present in Holt, Garfield, Rock, and Brown counties, and along the northern boundary of the sandhills in Cherry and Sheridan counties. These tracts are typically covered by a plant cover which is much less open than the bunch-grass land although here and there both of the dominant species show a poorly defined bunch-grass nature. The association presents a noteworthy landscape when the spear-grass is in fruit. The scattered stems with their multitudes of straw-colored or whitened awns waving in the wind above a loose or tufted sod appear from a distance not unlike a thinly stocked wheat field at harvest time. *Koeleria cristata* is one of the commonest grassy associates. Other grasses of importance in this association as it occurs outside the sandhills are *Agropyrum pseudorepens* and *A. spicatum,* but they are not commonly seen in the sandhills variation of the association.

Secondary species are found in considerable number. Within the sandhills proper some of these are those that hold a similar rank in other associations already described, while others are important and conspicuous only within this association in its typical expression westward. One of the most widespread species is *Monarda citriodora* which forms extensive societies characteristic of the sandy plains along the western border of the sandhill region in

Sheridan and Box Butte counties. Pound and Clements report that this species is also abundant on "the dry, flat, sandy stretches in McPherson County." Many of the gaily-colored legumes such as *Aragallus lamberti* and *Lupinus plattensis,* as well as *Pentstemon albidus* and *P. acuminatus,* are frequent and abundant members of this association as it is seen toward the western limits of the sandhills.

As we go eastward many of the distinctive secondary species drop out and bunch-grass interstitials come in with greater frequency. The *Stipa* hills of Holt County for instance do not exhibit any such kaleidoscopic changes so noticeable farther west during the spring and early summer because of so many brightly colored species in the high plains type of this association.

THE WIRE-GRASS TRANSITION ASSOCIATION

The wire-grass transition association as here delimited is somewhat like the "Beard-Grass Formation" of Pound and Clements and also similar to the "wire-grass association" of the "Short-grass Formation" of Shantz. The association is clearly intermediate between the typical prairie-grass formation and the typical short-grass formation, but within our limits its relationship is more clearly shown with the former. Farther westward the relation is undoubtedly more strongly with the short-grass formation as has been shown by Shantz (60) in his studies of Great Plains vegetation.

Composition of the Wire-Grass Transition Association

DOMINANT SPECIES

Aristida basiramea
Aristida longiseta
Aristida purpurea
Sporobolus cuspidatus

PRINCIPAL SPECIES

Bouteloua curtipendula
Bouteloua hirsuta
Bouteloua oligostachya
Bulbilis dactyloides
Cactus viviparus
Psoralea argophylla
Psoralea tenuiflora
Stipa comata
Stipa spartea

SECONDARY SPECIES

Allionia linearis
Andropogon scoparius
Aristida oligantha
Carduus undulatus
Chrysopsis villosa
Eatonia obtusata

Eriogonum annuum
Euphorbia petaloidea
Euthamia graminifolia
Festuca octoflora
Froelichia floridana
Gaura coccinea
Helianthus petiolaris
Hymenopappus filifolius
Ipomoea leptophylla
Koeleria cristata
Lacinaria punctata
Malvastrum coccineum
Meriolix serrulata
Opuntia fragilis
Opuntia polycantha
Parosela aurea
Psoralea lanceolata
Sideranthus spinulosus
Silphium laciniatum
Talinum teretifolium

The wire-grass transition association is best developed about the margins of the sandhill region upon soil less sandy than that of the bunch-grass association but not so firm or clayey as that of short-grass land. The widest stretches of the association are to be found toward the southwestern limits of the region and again in certain places along the Niobrara River north of the region proper. Shantz reports (60) that when the wire-grass occurs in eastern Colorado it is also found bordering sandhill areas.

As would be expected from its intermediate character this association partakes of the floral characters of the two closely related plant formations. These similarities are especially noticeable as we compare the secondary species of this association with those of the bunch-grass association and of the short-grass formation. The dominant species of this association are adapted to a much firmer substratum than that of the bunch-grass association, and the secondary species that are common in the two associations are those that prefer relatively quiet or clayey soils. This is a well-known characteristic of the principal species of this association as well. The tendency toward bunch-grass conditions is seen in the presence of *Andropogon scoparius, Psoralea lanceolata, Bouteloua hirsuta*, and *Eragrostis trichodes.* The tendency toward short-grass is shown by the other *Boutelouas* and *Bulbilis* as well as by a number of the secondary species. A notable relation to the more eastern conditions is shown by the presence of *Koeleria, Stipa spartea*, and *Silphium laciniatum.*

Typically the ground tone of the association is given by a carpet of *Bouteloua* which is, however, more open than that so characteristic of the short-grass formation. The wire-grass occurs in low tufts or close bunches of slender, light buff-colored or silvery stems scattered over this cover. The interval between the bunches

varies from three or four inches to several yards. Quite naturally when these intervals become great the presence of the true short-grass condition becomes emphatic, and this appears to be one of the reasons why Shantz has included this as one of the short-grass associations. The more open character of this association as it occurs with us, which is well indicated by the number of secondary species,

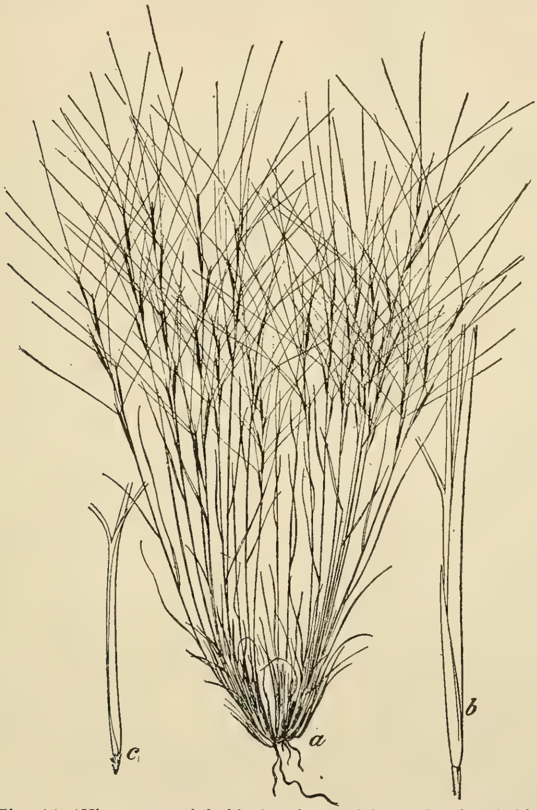

Fig. 14. Wire-grass, *Aristida longiseta*. Plant, showing habit, *a*; spikelet, *b*; flowering glume, *c*. (From Shantz.)

stands in sharp contrast to the closer association as seen in the typical expression of the short-grass formation.

Toward the northern and eastern portion of the sandhill region *Aristida purpurea* and *A. basiramea* are the usual controlling species of this association. On the southwestern border *Aristida longiseta* is the commonest species seen in the association where it comes in closest contact with the short-grass formation.

Shantz has shown in his Colorado studies (60) that the physical conditions in the "wire-grass association" are such as to "permit the growth of both shallow-rooted and deep-rooted plants. The shallow-rooted species are chiefly short-grasses which obtain most of their water supply from the first foot of soil." Being sandier than the soil within the grama-buffalo-grass asociation, water penetration is greater and run-off is doubtless less so that a greater quantity of available soil-moisture is to be had at considerably deeper levels within this association. This fact probably accounts for the presence of many of the deep-rooted perennials of this association which are lacking in the grama-buffalo-grass association. Wire-grass itself is a much deeper-rooted plant than the typical short-grasses. Shantz has further pointed out that "the presence of short-grass here indicates a condition unfavorable to the greatest development of the taller, deep-rooted plants. If the water supply were increased the latter would undoubtedly entirely replace the short-grass and the vegetation would probably pass over into the bunch-grass association. The amount of water available below the first foot of soil determines the number of deep-rooted plants which can develop. Since in the wire-grass association this amount is not sufficient to produce a dense growth of such plants, inter-spaces are left which are occupied by the shallow-rooted short-grasses. The presence of the short-grasses further reduces the amount of moisture available to the deeper-rooted plants but can not crowd them out entirely. . . . A condition of unstable equilibrium therefore exists, being more favorable for deep-rooted plants during wet years and more favorable for the short-grasses during dry years." It appears from a preliminary study of this association in our state that the above prophecy is probably correct. Here where the precipitation is considerably higher (toward the east about 10 inches greater) the number and frequency of the deeper-rooted species are apparently greater than in eastern Colorado. As to whether the final stage will be short-grass or some prairie-grass association can not yet be said, although it appears that one of the better-sodded associations of the prairie would be the more likely successor to the wire-grass transition association.

The Short-Grass Formation

The short-grass formation is poorly represented in the sand-hill region of Nebraska because of the relative absence of the soil

and climatic conditions that to a large degree govern the distribution of this typical Great Plains plant formation. Within the sandhills the formation occurs in widely scattered islands and tongues in various parts of the region where it has succeeded in pushing eastward among the prairie-grass associations. The total area occupied by this formation in the sandhills is very small as compared with that covered by the prairie-grass associations. In mixture with the wire-grass transition association short-grass is to be found far eastward along the northern border of the sandhills and in many places here the fairly typical short-grass formation is seen. Shantz has pictured in an admirable manner the eastward extension of these outposts of the short-grass formation of the Great Plains Area to central Nebraska where they meet the prairie-grass formation, the nature of which, as it occurs in the sandhills, has already been discussed. A very good conception may be gained of the situation with which we are dealing if we picture a broad vegetative background composed chiefly of the bunch-grass and blow-out associations over the uplands in almost all portions of the sandhills in practically unbroken continuity except for the relatively small and widely scattered islands, tongues, and belts of short-grasses, the one with a strong eastern affiliation and the other with a decidedly western tone. We have as it were the meeting and overlapping of two divergent vegetative frontiers whose foci are widely separated. Naturally then we find that the short-grass formation becomes increasingly noticeable as we pass westward through the hills until we finally leave the sandhills with their prevailing prairie-grass landscape and finally enter the arid short-grass region of the high plains.

The soil-moisture content of short-grass land is typically lower than that of any of the prairie-grass series and the non-available water (as determined by the wilting method) is much higher than in the bunch-grass land. Preliminary studies have been made upon the penetration of precipitation into the two kinds of soil and it has been found that this process is very much more rapid in bunch-grass land than in short-grass land. Run-off from these soils differs in the reverse relation. Shallow-rooted species are doubtless favored by these facts which may also account for the absence of many of the deeper-rooted secondary species that are characteristic of the bunch-grass association where soak-in is great and where there is a perpetual supply of moisture below a depth of a few inches.

Shantz has shown that the run-off from this association as it

occurs in eastern Colorado is great and that even during periods of more than normal rainfall available soil-moisture is limited to a few inches of the surface soil. He feels that it is because of this fact that "the vegetation is composed of short grasses which have a great number of roots limited to the surface foot or so of the soil. Most deep-rooted species are then shut out by lack of soil-moisture in the deeper layers of the soil and later-season plants are excluded because available moisture is usually lacking, even in the surface layers, during later summer and autumn." The surface soil becomes extremely dry and hot shortly after midsummer so that from this time there are very few species but the dominants to be found in the formation. All of the more conspicuous principal and secondary species except the cacti have disappeared by the fourth week in July.

THE GRAMA-BUFFALO-GRASS ASSOCIATION

The most typical form of the short-grass formation is represented by the grama-buffalo-grass association. If that portion of the sandhills covered by the bunch-grasses is monotonous, then this association presents a case of extreme monotony. This is the most typically closed association of the sandhill uplands and this condition, which prevents the establishment of many secondary species, is the cause of the extremely monotonous appearance of the short-grass formation. The dominant plants are low and closely matted in many places so that the ground is completely covered. Frequently, however, the carpet-like cover and close tenacious sod are broken here and there and within these light-colored soil areas certain additional species become established or bare patches alternate with the low patches of grasses. The grama-grass when growing alone occupies somewhat more sandy soil and produces a more open carpet than does the buffalo grass. When the latter species occurs alone, as it often does in characteristically circumscribed patches, the ground is covered by a mat so close that extremely few secondary species are enabled to establish themselves within such areas. It is probably because of this close growth of shallow-rooted species together with a lower available soil-moisture that the secondary species of this association and of the formation as a whole are much fewer in number than is true for the prairie-grass formation.

COMPOSITION OF THE GRAMA-BUFFALO-GRASS ASSOCIATION

DOMINANT SPECIES

Bouteloua oligostachya	*Bulbilis dactyloides*

PRINCIPAL SPECIES

Aragallus lamberti[1]	*Festuca octoflora*[1]
Aristida longiseta	*Plantago purshii*[1]
Bouteloua curtipendula	*Psoralea argophylla*

SECONDARY SPECIES

Allium nuttallii	*Hedeoma hispida*
Argemone intermedia	*Lacinaria punctata*
Aristida oligantha	*Malvastrum coccineum*[1]
Artemisia canadensis	*Monarda citriodora*[1]
Artemisia frigida	*Munroa squarrosa*
Astragalus mollissimus	*Opuntia fragilis*
Cactus viviparus	*Opuntia polycantha*
Croton texensis	*Psoralea tenuiflora*
Cucurbita foetidissima	*Schedonnardus paniculatus*
Eriogonum multiceps	*Sideranthus spinulosus*
Grindelia squarrosa	*Talinum teretifolium*
Gutierrezia sarothrae	

[1] Forming patches or communities.

The most striking variation produced in the general monotonous, often more or less parched, background of grama-buffalo-grass association is produced by the presence of patches wherein some of the secondary species are dominant and completely overshadow the short-grasses. Sometimes these areas are of considerable size and frequency so that the short-grasses lose to a certain degree their overpowering influence. In the sandier situations, for instance, the *Aristidas,* or *Stipa,* or even *Andropogon scoparius* may become so numerous as to change completely the nature of the vegetative cover, yielding a type of vegetation that would be difficult to classify or relate to any of the better-defined associations.

During the latter part of May or early June many of the more open, somewhat sandy areas of this association, especially as it is found in certain dry valleys to the westward and along the Middle Loup River, are covered by dense communities of *Festuca octoflora.* When the plants of this short-lived species first appear they are of a bright green color so that the areas thus dominated appear as promi-

nent color contrasts against the dull or somber gray of the grama-buffalo-grass setting. Pronounced color changes mark the ephemeral life-history of these communities. The initial green is gradually lost with the decomposition of chlorophyll and the development

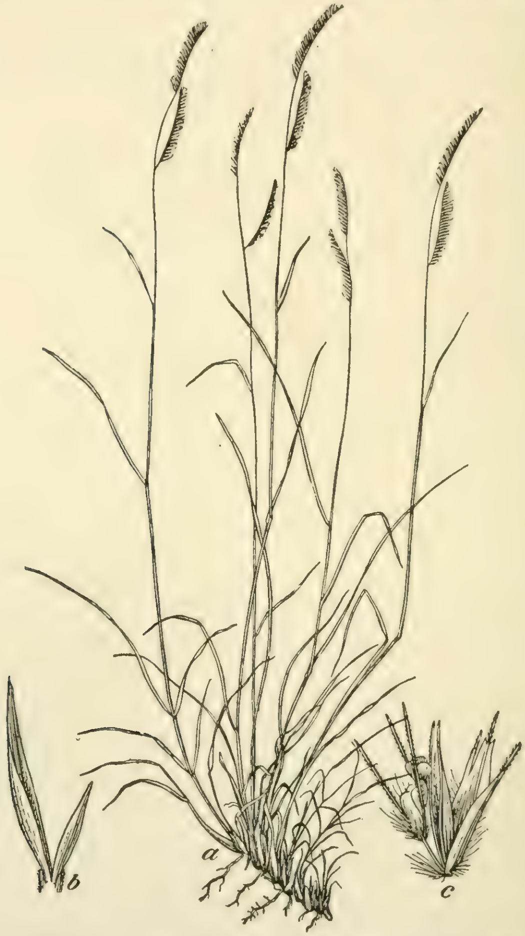

Fig. 15. Grama grass, *Bouteloua oligostachya*. Typical plant, *a*; empty glumes, *b*; perfect and imperfect flowers, *c*. (From Shantz.)

of a bright, clear straw color. Only a few days later the same plants have changed their color to a light brown, which finally, after a few more days, gives way to a most beautiful reddish-brown. These changes are brought about more rapidly during a dry season

when the water-content of the surface soil is being rapidly diminished. The same species is sparsely scattered over the hills but nowhere does it assume the importance that typifies its habit in this association.

Veronica perigrina, frequently developed in great abundance,

Fig. 16. Buffalo grass, *Bulbilis dactyloides.* Pistillate plant, *a*; staminate plant, *b*; pistillate spike, *c*; staminate spikelets, *d*. (From Shantz.)

is an earlier vernal occupant of the same areas that are later controlled by the *Festuca.*

So also *Plantago purshii* and *Lepideum apetalum* are often seen scattered through the association at the time the fescue grass is at its height. The patches of *Plantago* are especially noticeable

because of the low, silvery, silken plants that often become densely aggregated with a height about equal to that of the short-grasses. The pepper-grass and the plantain are two species that often invade the dense patches of *Bulbilis*. All of these variations are evanescent and the association is soon again characterized by that stability and monotone that is so notable for short-grass land.

The early summer, however, brings on societies of deeper-rooted species that persist for a longer period. One of the commonest of these is the *Psoralea argophylla* society which often covers acres of ground with bushy silvery plants about one foot in height. As indicated above the *Aristidas* also aid in the local obliteration of the short-grass appearance. Frequently these species develop a growth-form that reminds one of the bunch-grasses of the sandy hilltops. The bunches here are, however, always lower and silvery or, as in *Stipa*, very open and spreading. *Psoralea argophylla* is about the last species of the season partially to mask the short-grasses over any considerable areas. This species is also frequent in the bunch-grass association but in such habitats it never becomes social.

Other plants that are commonly seen in greater or less degree of aggregation are *Dyssodia papposa*, *Opuntia polycantha*, and *Monarda citriodora*. The prostrate, radially spreading vines of *Cucurbita foetidissima* are frequently seen by the traveler on the plains as an odd additional species of this association. The large, thick, dark-green, triangular leaves following out two to a dozen separate, sprawling branches radially disposed, produce a variation in the tone of the association that always compels notice. Again the tall bushy plants of *Psoralea tenuiflora* occurring as scattered individuals are noticeable because of their overshadowing tendency. This species often breaks off near the ground level and becomes a "tumble weed." Shantz notes that where this species is distributed uniformly it is indicative of "either a soil which is more easily penetrated by water than normal short-grass land, or else a place that receives the run-off from an extensive area which consequently is penetrated by more water than that which falls upon it as rain." Extensive stands of this sort are not found within the association as it occurs in this state, but lesser communities are common which according to the above investigator indicate "pockets of looser soil or depressions into which water drains from surrounding areas."

The Woodland Formations

There is an extremely small amount of woodland vegetation to be found in the sandhills. The arborescent plant life found here represents associations of woodland species that have migrated via stream courses from the woody formations to the east or west. Furthermore the species represented in these associations are greatly reduced in number and the individual plants are as a rule conspicuously smaller than those found in similar combinations nearer the centers of development of the eastern and western contingent. Although the woodlands of the sandhills are meagre it is a noteworthy fact that the invasion of numerous secondary woodland species has been made possible only along the above lines of migration, and that to-day we find many such species that have penetrated far into the region.

There are two kinds of forest or woodland formations to be seen along the streams of the sandhill region. One of these is essentially a *broadleaf* combination represented by narrow belts or tongues of tree growth that have pushed westward via stream courses from the wooded bluff region contiguous to the Missouri River. It is therefore seen that this type is related to the great climax mesophytic broadleaf forests of the Mississippi-Ohio valley forest complex. The other, less frequent and typical, is of a *coniferous* nature representing the easternmost extension of the *coniferous* forest complex of the Black Hills and Rocky Mountains. Both types of woodland follow stream courses into or across the hills, never wandering far from the immediate valley or canyon with its narrow flats or bluffs and ridges. The topographic features of the stream courses of the sandhills have already been indicated.

The Broadleaf Forest Formation

One of the most prominent geographic facts in regard to the sandhills is that many spring-fed streams of constant volume rise in the northern portions of the region, follow a northerly course, and finally enter the Niobrara, while few such streams come to the same drainage course from the harder land north of this main river of northern Nebraska. The reason for this difference is probably found in the relative absence of large areas of water-soaked sandhills to the northward. The soil there is mostly firm and clayey of the nature of short-grass land so that run-off is great and soak-in

little, and as a consequence there are few springs for the development and upkeep of streams.

The broadleaf forest formation reaches its maximum expression for the sandhills along these streams which emerge from the northern boundary of the region from central Cherry County eastward. The same general type of vegetation prevails as a frequent, although often disconnected, characteristic of the lower portions of the Loup and Dismal rivers farther southward. Pound and Clements have indicated (57) that this formation, which they called "The Springbranch Canyon Formation," represents certain modifications of the woodlands along the Missouri River with which it is directly connected by means of the courses of the sandhill rivers all of which eventually pour their waters into the Missouri. The above writers regarded this formation as a modification of "the bur oak-elm-walnut formation" of the Missouri River woodlands. The modification is mainly one of simplification.

Notable differences occur in the composition of the woodlands as we pass from the Missouri up the Niobrara and enter an increasingly drier region. Some of the characteristic tree species of the east, such as *Ulmus americana* and *Quercus macrocarpa,* decrease in abundance, and the growth of other woody plants becomes considerably dwarfed. This tendency toward nanism is a striking character of a number of woody species as we pass farther and farther westward. The increasingly scrubby form of the bur oak, *Quercus macrocarpa,* has caused the application of the common name "scrub oak" to this species. The green ash, *Fraxinus lanceolata,* also becomes remarkably dwarfed as compared with its growth farther eastward. Many species become dwarfed and infrequent along the lower 100 miles of the courses of the Niobrara and Loup, while other trees become less abundant until finally, when the sandhills are reached, the dominant species are quite different from those that control the Missouri River woodlands, and the forest is greatly reduced. The species that are most conspicuous in this formation in the sandhills are *Tilia americana, Ostrya virginiana, Fraxinus lanceolata,* and *Juniperus virginiana.* These trees are of sufficient importance in the formation in many localities as to produce a well-defined association.

THE LINDEN-CEDAR-IRONWOOD-ASH ASSOCIATION

By far the greater portion of the woodland formation is domi-

nated by the linden-cedar-ironwood-ash combination. This is similar to the subdivision called the "Linden-Cedar-Ironwood Formation" in the Phytogeography of Nebraska.

Because of the narrowness of many of the springbranch canyons the trees are frequently more abundant upon the higher slopes and bluffs about the canyons than deep down near the very narrow canyon bottom. The ironwood is often found in its characteristic low, dense aggregation upon the lower more shaded slopes as well as more scatteringly in almost every situation. The dominants are, however, as a whole distributed more evenly over the upper slopes and margins of the canyons.

Composition of the Linden-Cedar-Ironwood-Ash Association

DOMINANT SPECIES

Fraxinus lanceolata	*Ostrya virginiana*
Juniperus virginiana	*Tilia americana*

OTHER COMMON TREES

Acer negundo	*Salix amygdaloides*
Celtis occidentalis	*Salix longifolia*
Gymnocladus dioica	*Ulmus americana*
Juglans nigra	*Ulmus pubescens*
Populus sargentii	*Ulmus racemosa*
Quercus macrocarpa	

THE SHRUBBERY LAYER

Cornus amomum	*Rhus radicans*
Crataegus occidentalis	*Ribes gracile*
Euonymus atropurpureus	*Sambucus canadensis*
Opulaster opulifolius	*Xanthoxylum americanum*

EXTRA-FORMATIONAL THICKETS

Amelanchier alnifolia	*Rhus glabra*
Amorpha fruticosa	*Rhus trilobata*
Cornus asperifolia	*Ribes aureum*
Cornus stolonifera	*Rubus occidentalis*
Lepargyraea argentea	*Salix longifolia*
Prunus americana	*Salix nigra*
Prunus melanocarpa	*Symphoricarpos occidentalis*

LIANAS

Clematis ligusticifolia	*Smilax herbacea*
Parthenocissus quinquifolia	*Vitis vulpina*

The dominant species are developed to about the same height, a tendency which results in the production of a rather uniform layer. The only exceptions to this rule are seen in certain habitats where *Ostrya* becomes very tolerant and develops as a decidedly pronounced under story, and again in the broad and more open parts of the canyons where considerable alluvium has accumulated and where the uniformity of height growth is broken by the presence of a few very large and tall specimens of *Populus sargentii, Juglans nigra, Ulmus americana,* or *Tilia americana*. These species frequently reach a development that compares well with that seen in the maximum broadleaf woodlands upon the alluvial deposits near the Missouri River.

Mingled with the dominant species are to be found a few other tree species in almost all of the canyons. For instance *Celtis occidentalis, Ulmus pubescens,* and *Gymnocladus dioica* are common and reach about the same height as the uniform forest of controlling species. *Acer negundo* is a frequent additional species that in some places reaches an abundance almost equalling that of some of the dominants.

Along the Dismal and Loup rivers this association does not reach as highly developed a state as that characteristic of the Niobrara and its springbranch tributaries. This is probably to be expected since these points are much farther from the Missouri woodlands. The ironwood and the linden are much less frequent here and when found are never in the abundance that is typical for the northern streams. At present *Fraxinus lanceolata* is by far the most characteristic and abundant member of the dominant species of this association as it occurs along the Dismal and the Loup rivers. These streams follow a much broader valley for the most of their course than that which marks the springbranches in the north. The steep-sided canyon with rocky walls is the exception rather than the rule along the Dismal and Loups which follow an extremely meandering course through the hills. Fires and the axe have had a marked effect upon the woods of these rivers so that at present they exhibit a distinctly patchy appearance. At one time the number of red cedar and ash trees along these streams was much greater than at present as is told by the stump remnants. Along the rivers the woodlands are usually found occupying poorly defined benches in the form of long narrow belts or patches of a few acres in extent. In many places the woods have been reduced to a very narrow belt

which closely fringes the stream. The hackberry and ash are especially common in this form.

At the present time along the Dismal the red cedar is reproducing and extending its range to a noticeable degree. The distribution of the species is characteristically high up on the canyon or bluff sides and in such sites, where there are "breaks" or young canyons in the firmer argillaceous soil, the cedar is abundant and appears to be leading its way out over the surface of these rough places with considerable rapidity. Red cedars are much rarer along the Loup rivers where they now occur singly or at most in scattered groups of few individuals in sites very like those where the species is much more abundant along the Dismal.

A shrubby layer is poorly developed beneath the trees of this association. *Sambucus canadensis, Cornus amomum, Ribes gracile, Rhus radicans,* and *Symphoricarpos occidentalis* are the commonest species of the shrubby layer and some of these species are very infrequent. For instance *Cornus amomum,* which forms thickets beneath the trees of the springbranches of the north, has not been found farther south.

The characteristic shrubby growth of the *hills* is seen in the form of *extra-formational thickets* along the larger streams. *Rhus glabra* is a constant member of such thicket associations in many parts of the hills. The species is found in great abundance along the Middle Loup and the Dismal beneath the more open forest cover as well as in the form of highly developed marginal thickets. The sumac exhibits the same extra-woodland aspect here that is so typical of its distribution over the bluffs of the Missouri where it is the almost ever-present forerunner of the forest. Extending from beneath the scanty woodlands of the Dismal and Loup rivers numerous species of shrubs are to be found disposed in the form of dense marginal thickets. From such sites these species spread to a wide range of sites over the bluffs and far back into the hills. These woody species are differentiated into two groups dependent primarily upon soil-moisture. Across the lower portions of the canyons or river valleys where the sandy soil is quite moist such species as *Amorpha fruticosa* and *Salix longifolia* form areas of bush-land from 6 to 10 feet in height and many acres in extent. Species that are common in similar to drier sites are *Cornus stolonifera, Sambucus canadensis, Salix amygdaloides,* and *Xanthoxylum americanum.* Where the soil is somewhat drier, but with the water

table within a few inches of the surface, an extremely dense, and in many places impenetrable, bush is developed by an association of *Prunus americana, P. melanocarpa, Ribes aureum, Crataegus occidentalis,* and *Lepargyraea argentea* in various degrees of mixture. Thickets of this sort often cover many acres of the harder land upon river flats not occupied by grasses. Along the Niobrara scrubby individuals of *Quercus macrocarpa* enter into the formation of somewhat similar, though more open, thickets. *Rhus radicans* is very commonly present as a secondary layer in both types of thickets, and the low much-branched and interlaced crowns of the dominant species are often rendered still more dense by the copious development of the four lianas, *Parthenocissus quinquifolia, Vitis vulpina, Clematis ligusticifolia,* and *Smilax herbacea.*

It frequently happens in those places where there is a wide interval of comparatively hard land between the stream and the first hills that the above bushland is bordered by a belt of lower, finer, wirelike bushes lying between the taller thickets and the bases of the hills. This belt, most often composed of *Symphoricarpos occidentalis,* is a pronounced vegetative feature of river flats in many places, especially along the Middle Loup and the Dismal. *Rosa arkansana* is frequently mingled in great abundance with the "buckbrush." The former species often forms exclusive communities which alternate with similar patches of the latter. These distributional relations are often emphasized upon the dry river flats of the Middle Loup, especially where distinct belts are developed according to the above sequence.

Peculiar modifications of the thicket are common far back in the hills away from the taller woodland species. The species that most commonly leave the neighboring fringe of woods are *Symphoricarpos occidentalis* and *Prunus americana.* The former typical border plant occurs in very close stands of individuals about two feet in height in many of the "pockets" and dry valleys. Frequently the floor of a dry valley is covered for many acres by this species alone or in mixture with *Rosa arkansana,* a regular member of the bunch-grass association. Smaller "pockets" or basins with a complete cover of this sort are especially conspicuous interruptions of the usual grassy tone of the uplands. Such stands of bush are often so dense as to exclude nearly every other species. The "buckbrush" has been carried into almost every part of the region and one may come suddenly upon such a "buckbrush pocket" in the bunch-grass

association many miles from any woodland. The plant is seldom seen upon exposed hilltops since it can not endure serious wind action. The wild plum is also commonly seen in similar isolated situations more or less completely surrounded by bunch-grasses. *Prunus melanocarpa* is likewise present in low bushy form in many sites away from the streams.

A species with a decided tree-form that occasionally develops similar circumscribed patches in the "pockets" among the driest hills is *Celtis occidentalis*. I have seen "hackberry pockets" with a clump of about a hundred trees ranging in diameter from 1.5 to 8.0 inches and with a uniform height of 18 to 20 feet. Woodland birds build their nests here far from the larger bodies of timber. The most notable use of the "hackberry pockets" by birds is by the great blue heron, *Ardea herodias*. These large birds take almost complete possession of some of these groves and use them as nesting places for many generations.

The peculiar distribution of all of these species over the uplands away from the woodlands is doubtless related to the influence of birds in seed carriage.

Both xerophilous and mesophilous herbs are numerous within the shade afforded by the trees of this association, as well as in fewer numbers scattered through the various thickets briefly noted in connection with the woodlands. The commonest of these are included in the following alphabetical lists without regard to abundance, frequency, or layerage.

HERBACEOUS SPECIES IN OR NEAR SANDHILL WOODLANDS

SPECIES OF WIDE DISTRIBUTION

Adicea pumila
Agrimonia stricta
Apios apios
Aster salicifolius
Bromus ciliatus
Carduus altissimus
Carex longirostris
Celastrus scandens
Circaea lutetiana
Elymus canadensis
Filix fragilis
Fragaria americana
Galium aparine
Galium triflorum
Geum canadense
Geum strictum
Homalocenchrus oryzoides
Humulus lupulus
Koellia virginiana[1]
Lappula americana
Macrocalyx nyctelea[1]
Moehringia lateriflora
Monarda fistulosa[1]
Muhlenbergia mexicana

Muhlenbergia racemosa
Nepeta cataria[1]
Oryzopsis micrantha
Parietaria pennsylvanica
Phryma leptosepala
Polygonum sagittatum
Polygonum scandens
Sanicula canadensis
Solidago canadensis
Stipa viridula
Thalictrum purpurascens
Urtica gracilis[1]
Vagnera stellata[1]
Washingtonia longistylis

SPECIES MORE COMMON NORTHWARD

Aralia nudicaulis
Arisaema triphyllum
Boehmeria cylindrica
Campanula rotundifolia
Elymus striatus
Erysimum cheiranthoides
Falcata pitcheri
Heracleum lanatum[1]
Heuchera hispida
Impatiens biflora[1]
Lobelia syphilitica
Salamonia comutata
Silphium perfoliatum
Thermopsis rhombifolia

[1] Forming patches or communities.

It will be appreciated at once after an inspection of these lists how closely the above species agree with common woodland species farther east. The absence of many of the species that are noted in the Missouri woodlands is also conspicuous.

THE PAPER BIRCH ASSOCIATION

Following in the wake of the retreating ice cap that covered eastern Nebraska during Pleistocene time, there rolled northward over the state a great boreal floral wave. As the ice receded farther and farther northward nearly all of the boreal species, left thus for a time in a less polar climate, eventually migrated far beyond the northern limits of the state. One of the most notable examples of a plant that was left within our borders when this retreating floral wave carried so many species northward is the paper birch, *Betula papyrifera*. This species has become perfectly established in the cool, box-canyon-like ravines which lead from the northern portion of the sandhills to the Niobrara River in Cherry, Brown, and Rock counties.

The most common type of woody vegetation in these spring-branch canyons has already been noted in the preceding association. However, in a number of such canyons and at many places the paper birch exerts a decidedly controlling influence in association surrounded by other trees of such woodlands. The usual Missouri

valley trees already noted are present as in similar canyons without the birch.

Aside from the presence of the birch with its poorly developed secondary layers the canyons are about the same as has been indicated in the former association. The usual thickets of *Prunus, Symphoricarpos, Rhus,* etc., are to be seen over the upper and outer stretches of the canyons and these in turn soon give way to one of the upland grass associations.

The surface conditions in the birch springbranch canyons are well described by Pound and Clements (57) as follows: "The lower canyon sides and the banks of the streams are covered with a very deep layer of humus and leaf mold, and are strewn with fallen trunks of paper birch. Over all grows a uniformly dense carpet of mosses, *Funaria, Mnium, Bryum,* and *Hypnum,* which constitutes the sole layer of the deeper, wetter portions of these canyons. Scarcely less characteristic than this dark green, mossy layer is the well-developed layer of large fleshy fungi, *Lactarius, Clarkeinda, Helvella, Geoglossum,* and *Peziza,* and of small cup fungi, *Sepultaria, Barlaea, Humaria,* etc."

The more open portions of these springbranch woodlands where erosion has swept away the most of the humus, as on the upper slopes and rims, are often characterized by a scattered, tufted carpet of *Selaginella densa.*

The Yellow Pine Formation

This formation, with a distinctly western alliance, brings into the state our only native pine, *Pinus ponderosa* var. *scopulorum.* This is a variety of the western yellow pine which occurs in such conspicuous abundance in the Rocky Mountains and the Black Hills. The formation in our state is developed to the highest degree upon the ridges and upper slopes of "Pine Ridge." Pine Ridge is an *escarpment* which enters the state near the northwest corner from Wyoming and extends eastward as a narrow tongue approximately parallel with the northern state line. This northerly facing scarp cut through the Loup Fork Beds has been greatly eroded so that the "ridge" is in reality a complex of deeply cut canyons, often with precipitous sides, varying from a mile to several miles in length, which originate in the high short-grass or spear-grass covered plains to the southward and make their way through the scarp at

approximately right angles to the general trend of the scarp. The heads of these canyons are sometimes several hundred yards above the outlets from which flow numerous clear streams northward toward Hat Creek and White River.

The maximum development of the yellow pine formation is to be found upon such canyon sides as they occur in Sioux and Dawes counties. Similar stands occur farther south in Scottsbluff and Banner counties but these areas do not enter the sandhill region. Eastward from Sioux and Dawes counties the abundance of the yellow pine rapidly decreases as the "ridge" becomes lower and narrower. The species is, however, found in great frequence, and is often locally abundant much farther eastward upon the extremely xerophilous ridges and cliffs of the Niobrara River and its tributaries. The species continues in gradually diminishing rate across Cherry county and as far eastward as Brown and Keya Paha counties, about 280 miles east of the Wyoming line where it enters the state. A remarkable correlation exists between the soil of the Loup Fork Beds and the distribution of this tree. The greatest expression of the species is always seen where there is the greatest quantity of these rocks exposed or where they lie near the surface.

Toward the eastern limits of its distribution along the Niobrara, the western yellow pine meets and mingles with the species of trees from the central hardwoods region of the east that have already been noted as occurring in the canyons of the Niobrara and its tributaries. Thus we have the meeting and overlapping of slender arms of western and eastern forest centers along the northern border of the sandhills.

The yellow pine enters the sandhills by way of a number of the springbranch canyons which reveal also the characteristic broadleaf features described on preceding pages. One of the best instances of the entrance of the pine is seen along the Snake River, a stream which arises in eastern Sheridan County and flows eastward across northern Cherry County to a point somewhat east of the center of this county, where it turns sharply northward and cuts its way through the underlying rocks to the Niobrara. Along its lower course the Snake has cut a deep, narrow canyon with walls of Loup Fork rocks almost vertical in many places. Such conditions are found especially below the falls of the Snake about 30 miles southwest of Valentine. At this place the clear rushing stream about 50 feet in width leaps over a ledge in its bed and produces a waterfall

24 feet in height. The river lies about 400 feet below the tops of the surrounding hills which cap the rocks of the Loup Fork series at this point. At numerous places along the river the bunch-grass association with its very sandy soil approaches the brink of the canyon so closely that the sand sometimes rolls into the stream. The broadleaf woodland is well developed in the lower portions of the canyon where there is a sufficient width of the floor beside the stream to afford footing for the trees that control the association. Sometimes a tall pine is seen among such trees, but typically the conifer is seen only in extremely open distribution over the upper canyon slopes and bold ridges. The individual trees vary from 10 to 30 feet in height and, because of their isolation, they are commonly round-topped and branched to near the ground. The red cedar, *J. virginiana,* is also common here as widely scattered individuals. A number of trees of this species were seen that were as large as the largest pines.

Here, as in the typical broadleaf canyons, the common species of low shrubs are conspicuous. Thickets of *Prunus americana* and *P. melanocarpa* are found at many points in the canyon where the walls are not too steep. *Rhus glabra* is a common species of the canyon rim. *Rhus trilobata* is also frequent along these canyons where its characteristic low communities of 1 to 10 feet in diameter are common upon outcrops and new talus slopes. *Amelanchier alnifolia* is an additional member of the shrub layer, along with *Ribes aureum,* both of which are found in rock crevices toward the upper portions of the slopes. Herbaceous species of Pine Ridge flora are more or less frequent here. The commonest of these are *Arenaria hookeri, Paronychia jamesii, Orophaca caespitosa, Eriogonum flavum,* and *Campanula rotundifolia.* The latter species is confined to grassy slopes or the slight shade afforded by the open tree growth; the others are typical mat or rosette plants that are prominent species of rocky substrata.

Along the upper limits of this formation as it is seen in the sandhills the trees are widely scattered over bunch-grass or other grassy land with a sandy soil. Out of the canyon proper there are very few spots where the trees occur in sufficient density to shade out the grasses completely, and in general it appears that the invasion of the surrounding grassland by the pines is an extremely slow process, and it may be doubted if such invasion will ever progress far under the conditions existing at the present time.

A paper by Kellogg (44) contains some general studies of this formation which he terms the "pine type." These observations, which were made outside the sandhills, include the manner of growth, reproduction, rate of growth, and the economic value of the dominant species of this formation which has been very briefly characterized.

LOWLAND FORMATIONS

Extensive lowland plant formations are found in many parts of the hills. In general these do not differ fundamentally from similar groups of vegetation common farther east and all are to be regarded as invasions of typical aquatic, marsh, and meadow species that are not peculiarly characteristic of the sandhills.

For convenience in this preliminary study all of the lowland plant associations have been grouped under three formations, the water-plant formation, the marsh formation, and the meadow formation. I have included within the water-plant and marsh formations all of the hydrophytes and most of the helophytes of the sandhills. The third formation is composed of species that range from hydro-mesophilous forms to the more mesophytic species of the meadows.

The Water-Plant Formation

The water-plant formation occurs in the most pronounced and clearly defined form in the lakes and ponds that characterize certain portions of the region. Such hydrophilous centers are found, as has been indicated in a former subdivision of this study, in east central Cherry County; in southwestern Brown County; in southwestern Cherry County, at the headwaters of the Middle Loup River; in western Hooker County, at the head of the Dismal River; and in central and northern Garden County. Besides in these major centers the formation is often seen in cut-off ponds along the Dismal and Loup rivers. As a rule, however, the streams of the region are so swift that the water-plants are not often found in any considerable aggregation along their courses except in occasional protected bays. On the other hand many of the lakes and ponds of the region are literally chocked by the members of this formation which occur in extensive tangled colonies. The total volume of the water-plants varies somewhat from season to season. There are rather evident indications of a climatic control which may determine the relative abundance of species for different years.

The waters of practically all of the many ponds and lakes contain considerable quantities of saline and alkaline compounds. The quantitative nature of dissolved solutes in an aquatic substratum has been thought to exert an important relation to the specific composition and the distribution of hydrophytic and helophytic vegetation. Harshberger has shown (38) that the distribution of certain species of marsh plants on the New Jersey coast is governed very largely by the density of the water. Much study has centered about this question and much has been published (34, 50) bearing upon the quantitative and qualitative aspects of the problem.

From a mere surface view the waters of the sandhill lakes appear to differ considerably in alkalinity. Some such bodies of water are extremely brown and foamy. The latter nature is marked under the influence of a high wind when great windrows of white "suds" are blown upon the beach. Others not perhaps quite so deep-colored are soapy to the skin, while still many others exhibit a distinct amber color.

It was thought that the composition and quantity of some of these solutes might exert a controlling influence upon the distributional phenomena exhibited by the aquatic phanerogams of these lakes. Samples of the water from a number of the lakes were accordingly sent for analysis to the Coöperative Laboratory of the United States Department of Agriculture, Bureau of Soils, at Reno, Nevada. I am pleased to acknowledge my indebtedness to this laboratory for certain data which they have obtained and furnished me from analyses of the samples which were taken from the lakes in eastern Cherry County. The following table is chosen from these unpublished data.

DISSOLVED SOLIDS IN THE WATER OF CERTAIN CHERRY COUNTY LAKES

Sample No.	From	Per cent dissolved solids including organic matter
1	Small pond near 2	0.40
2	Big Alkali Lake	0.09
3	Phalaris Lake	0.12
4	Whitewater Lake	0.03
5	Little Alkali Lake	0.47
6	Dewey Lake	0.02
7	Clear Lake	0.17
8	Hackberry Lake	0.05

It will be noted that the concentration is not *great* in any case. The total amount of dissolved solids, including organic matter, is

not nearly as high as that in the alkaline lakes of other portions of North America. Quoting from correspondence with Dr. E. E. Free, of the above laboratory, it is seen that "the dissolved salts present are mostly carbonates. The proportion of potassium salts seems to be somewhat higher than normal but the waters are so dilute that the samples at hand are hardly large enough for an accurate determination of this element." A later letter from the same laboratory reported that calcium was not found in any of the samples; that potassium was present in all of the samples except number 5; and that numbers 2, 4, 6, and 8 show both sodium and potassium.

The most noticeable possible correlation between the dissolved solids and the vegetation of these lakes is that in the case of numbers 1, 3, 5, and 7 the submerged and floating aquatics are very greatly reduced. Species of *Potamogeton, Myriophyllum,* and *Nymphaea* are relatively infrequent in such lakes. There is a very pronounced difference in the abundance of all of the common aquatics in numbers 4 and 8. Number 4 showed fewer species and a much less abundance of submerged aquatics as compared with number 8, and yet the total dissolved solids in the two lakes differed by only 0.02 per cent. It may be, however, that the water of Whitewater Lake contains certain detrimental elements or ions that are lacking in Hackberry Lake. Nothing definite can be concluded in regard to this matter until we have made very extensive and complete quantitative and qualitative analyses of these waters, and have further supplemented these studies by data obtained from carefully performed cultural experiments. Even then, since the level of the lakes varies from season to season, and probably also the concentration and composition of the waters, it may be impossible to point out a clearly defined correlation in all cases.

The concentration of the waters of some of the lakes toward the western portion of the hills is higher than that noted in any of the above lakes. For instance Modesitt has published a brief note (48) which indicates that some of the lakes contain high percentages of dissolved salts. He found from analyses made by the same laboratory as noted above that the total salt content runs as high as 3.0 per cent in some cases, and that in one case 30.09 per cent of the total salt content was K_2O. Where the waters are so concentrated it is common to find, during dry seasons especially, a pronounced crust of crystalline material upon the beach of these

lakes. Modesitt dug a pit on the shore of one of these lakes over the top of which a crust was formed. He found that there were 47.72 g. of soluble salts in each 100 cc. of this crust when it was dried at 105° C.

THE PONDWEED ASSOCIATION

This association which is very frequent throughout the sandhill lake regions is characterized by the presence of species which are, in the main, similar to those of Warming's "limnaea-formations" or of the "Pondweed Formation" of Pound and Clements. Represented by one or more of the dominant species in an endlessly variable mixture, the association is found in greater or less degree in practically all of the ponds, lakes, and streams of the region. Notwithstanding the salinity of the water in some cases the species of this association are all typical of fresh waters.

As has been said the lakes are all shallow, and so as a rule the individuals of the various species are rooted at least a part of the time in a loose, sandy, or mucky soil at the bottom of the lakes. Typically this association is composed of plants which are completely submerged or at most possess floating leaves, as in the case of *Potamogeton,* some species of which are wholly submerged while others possess both submerged and floating leaves. Various methods of propagation characteristic of this kind of plant life are revealed by the species of this association, but these aspects will not be treated at length in this paper. The common types of stem and leaf morphology exhibited by the dominant aquatics need not be indicated in this study.

Composition of the Pondweed Association

DOMINANT SPECIES

Batrachium trichophyllum
Myriophyllum spicatum
Potamogeton foliosus
Potamogeton heterophyllus
Potamogeton richardsonii

PRINCIPAL AND SECONDARY SPECIES

Ceratophyllum demersum
Lemna trisulca
Polygonum amphibium
Potamogeton amphifolius
Potamogeton lonchites
Potamogeton natans
Potamogeton pectinatus
Potamogeton pusillus
Potamogeton zosteraefolius

Although no very careful detailed studies have been made of the distribution of these species, it appears from observations extending

over the greater portion of all of the lake centers of the region that such factors as relative depth of water, alkalinity, light, and clearness of the water, influence to some degree the distribution of the various species in the different lakes. The position of the aquatics within any given lake appears to be determined largely by chance dissemination. Movements of the water under the force of the wind may be the distributive factor in some cases, especially in the larger lakes that are more exposed to wind action than the slender finger lakes that lie between sheltering ranges of hills. Seldom does one see a species with floating leaves, such as *Potamogeton natans,* in the larger (though also shallow) lakes where wave action is most pronounced. The effect of light, though probably of primary importance in the vertical distribution of aquatic plants, is not clearly evident here. Alkalinity and turbidity, in extreme cases, are phases of the lake biology that are most pronounced. Until field methods for the determination of light values in water are far more perfect than at present, the relation of turbidity and of pigmented waters to the distribution of hydrophilous life must remain, as largely at present, great unknowns.

In many of the less alkaline or turbid lakes of the sandhills the above species often reach such density of growth in the form of extensive submerged beds that boating becomes difficult or impossible during late summer after the various species of the association have passed their maximum vegetative period. As one looks down into the clear water of the richer lakes the appearance of the vegetation is that of a tangled aquatic garden of low stature in which *Myriophyllum spicatum* and the *Potamogetons* are most commonly dominant. It is a rather notable fact in these dense aggregations of plants that the various species seldom become mixed to a marked degree. The tendency is toward the production of alternating pure colonies. Thus in rowing about one passes over such dense relatively pure communities of *Myriophyllum, Potamogeton richardsonii,* or *P. heterophyllus.* In the more open water one sees similar, but much more open aggregations of *P. zosteraefolius, P. natans,* and *P. pectinatus. Potamogeton foliosus* is most abundant in the alkaline waters where it often fills broad areas of shallow water with a dense grassy tangle to the exclusion of most all other plants. This is the one of the species of this association that appears to have solved the problem of alkali resistance to a remarkable degree, and it is seen in particular abundance in the hills wherever there are

alkaline lakes or ponds. In the shallower water where there are openings between the colonies of water-weeds *Lemna trisulca* is often developed in very pronounced cushions or beds sometimes three yards across, which because of their light, yellow-green color contrast boldly with the generally dark green or brownish surroundings.

Toward the western portion of the sandhill region *Batrachium trichophyllum* becomes a frequent, and often a very abundant member of this association. The water crowfoot groups might well be classed as vernal societies of the association under discussion. The species has usually flowered and passed its height of development long before the other dominants become conspicuous. This species is very common everywhere as a secondary species. When of controlling abundance *Batrachium* is one of the most showy plants of the whole state. I have seen the species so densely aggregated in some ponds and lakes that hundreds of square yards of water surface were concealed by the masses of showy, white to cream-colored flowers. The water areas dominated by *Batrachium* are typically old ecologically, or ponds in which there is a great accumulation of organic matter in the form of mud or muck from which for some reason or other the marsh formation is absent. The species appears to be rather plastic with reference to its water requirements, since it is found in abundance from the more open water to the relatively low water-content substratum of a late stage in the marsh or wet meadow. With *Batrachium trichophyllum* in such amphibious situations we commonly find such plants as *Roripa nasturtium, Cardamine hirsuta, Veronica americana, Mimulus jamesii,* and *Monniera rotundifolia.*

This association plays a well-known remarkable rôle in the preparation of a suitable substratum for later stages in the succession. As a result of the dense aggregation of the individuals of the constituent species, the bodies of water controlled by this association rather early exhibit a pronounced accumulation of débris consisting of the remains of former generations of aquatic plants and animals mixed with fine mineral particles brought in by wind and wave and effectively held in position by the expanding tangle. In this manner the accumulation of humus decreases the total amount of water in the substratum and the habitat approaches a little nearer the mesophytic. The soft oozy bottom is slowly raised by the accretion of humus and the substratum becomes relatively

drier and more compact. The continuation of these processes by aquatic plants finally results after many years, as Cowles (32) and others have emphasized, in preparing the way for their own elimination and the establishment of such plants as pond lilies and others with slender stems and floating leaves. Through the agency of further humus accumulation a suitable foothold is eventually afforded for the development of the bulrush and other members of the marsh formation. From this time the latter, very different stage in the vegetative cycle dominates the positions once held by the pondweeds until this type also is replaced by a still later phase of the succession.

THE WATER LILY ASSOCIATION

The usual position of this association, dominated by *Nymphaea advena,* in the vegetative cycle appears to be immediately behind or following the former association. This relation is sometimes seen in the sandhill lakes where the water lily occupies a belt lying between the pondweeds and the marsh species. Quite frequently, however, when the marsh formation is young and comparatively open the lilies are seen in considerable abundance among the rushes. In the latter case the lily is probably to be regarded as a relict. Under these conditions the "mixed association" is characterized by a more diffuse stand of rushes and the production of the condition that Tansley (66) has called "the *open* reed or rush swamp association." Probably because of the generally shallow water of these lakes the lily association does not always hold its normal position, but is more commonly found in the more open portions between the beds of submerged aquatics. The floating leaves almost completely cover the water in such places over areas many square yards in extent.

Additional floating-leaf aquatics are occasionally seen in mixture with the lily. The commonest of these secondary species are: *Potamogeton natans* in the deeper water and, where the depth is not so great, *P. lonchites* and *Polygonum amphibium* are common. With continued humus addition and elevation of the lake bottom the lily colonies become invaded more and more completely by *Scirpus, Typha* or *Phragmites* until finally the "mixed association" gives way completely to the dense aggregation of the marsh formation when *Nymphaea* disappears completely.

THE STONEWORT-NAIAD ASSOCIATION

This is a peculiar association revealed in some of the lakes and ponds of the region which are characterized by a broad belt of shallow water above an open sandy bottom. The association, composed of species of *Chara, Naias flexilis,* and *Zannichellia palustris,* sometimes covers the sandy bottom in such places with an open or more or less perfect carpet of tufted vegetation. The characteristic position of the association is in those quiet waters that sometimes lie between the shore line and a belt of rushes or reed-grass standing farther toward the open water of the lake. The association also invades to a certain degree the open bulrush-reed-grass association after the humus has for some cause been washed out thus exposing a comparatively bare sandy lake bed beneath clear shallow water. The tufted colonies of the above species are often very conspicuous as a distinct layer in such places. As a rule, also, there are quantities of algae of a number of species which coat the sand particles and pieces of débris that lie between the tufts of the dominant species with a rich color tone varying from deep blue-green to light yellow-green. Species of *Nostoc* and certain calcareous algae are often very noticeable here. Against this shallow, pebbled cover are seen the low tufts of the dark olive-green *Naias* or *Zannichellia* with their ericoid leaves. These tufts, composed of a few stems with a height of a few inches, occur scattered over the alga-strewn bottom at intervals varying in width from a yard down to a few inches where the densest aggregation was seen.

Other species that are occasionally seen with the above are *Ruppia occidentalis* and a peculiar submerged form of *Eleocharis acicularis.* The tufts of the latter are more strict than those of the other members of the association. The stiff, needle-like leaves gathered into close tufts stand up in a decidedly bristling manner. The growth of this species beneath the water is very different from that which typifies its habit upon the wet beach near the water line where it frequently forms local areas of dense sod.

A very different aspect of this association is seen in some of the small lakes and ponds in certain portions of the sandhills where the *Chara* phase of the association becomes so extremely abundant and voluminous as not only to control the situation, but to pack the waters with a dense wirelike tangle of harsh, calcified stems. This condition presents a peculiar type of closed alga association composed of a number of species of *Chara.*

The peculiar restricted distribution and composition of this association makes it very uncertain as to how the association should be considered in relation to the other aquatic and helophytic vegetation of the region. It appears to play little or no particular rôle in the regular successional relation between the associations of the open water or marsh. The slight humus-gathering ability possessed by the tufted species may be of some importance in relation to the invasion of these areas by *Sagittaria, Alisma,* and *Plantago.*

The Marsh Formation

The marsh formation is the most extensive and conspicuous vegetation unit of the sandhill lowlands, characterized by a saturated soil and often extending into the open water of lakes and ponds. Such areas, often many acres in extent, are always controlled either by *Scirpus validus, Phragmites phragmites, Zizania aquatica,* or *Typha latifolia,* or by mixtures of these dominant species. The most typical aspect of the formation, because of the relation of the formation to lake and pond phenomena, is found in the several lake centers of the region.

The regular position of the marsh formation is between the open water with the preceding formation and the meadow associations which lie between the marshes and the lower limits of upland vegetation. The transition from marsh to wet meadow, to relatively dry meadows, and finally to one of the upland associations is very easily appreciated in many places because of the regular belting that so often characterizes these various groups. Many areas occupied by this formation are to be seen that doubtless were formerly covered by open water and more or less filled with the pondweed formation. The common bulrush, *Scirpus validus,* is the most frequent of the dominant species. This plant occurs in characteristic dense, dark green stands about lakes and ponds, in wet valleys, and less abundantly along streams throughout the sandhill region. The formation as here regarded is similar in part to the "reed-grass-rush formation" of Pound and Clements.

THE BULRUSH-REED-GRASS ASSOCIATION

An association composed mainly of *Scirpus validus* and *Phragmites phragmites* is the most common subdivision of the marsh formation. These two dominant species often occur in extensive,

pure, alternating stands, as well as frequently in mixture, covering great stretches about the lakes and in old lake beds with a dense jungle of closely aggregated stems.

COMPOSITION OF THE BULRUSH-REED-GRASS ASSOCIATION

DOMINANT SPECIES

Phragmites phragmites	*Typha latifolia*
Scirpus americanus	*Zizania aquatica*
Scirpus validus	

PRINCIPAL AND SECONDARY SPECIES

Alisma plantago-aquatica	*Polygonum hartwrightii*
Asclepias incarnata[2]	*Potamogeton lonchites*[1]
Berula erecta	*Potamogeton natans*[1]
Ceratophyllum demersum[1]	*Rumex britannica*
Cicuta occidentalis[2]	*Sagittaria arifolia*
Eleocharis acicularis	*Sagittaria latifolia*
Eleocharis palustris	*Scirpus fluviatilis*
Myriophyllum spicatum[1]	*Scirpus pallidus*
Nymphaea advena[1]	*Spartina cynosuroides*
Phalaris arundinacea	*Stachys palustris*[2]
Polygonum amphibium[1]	*Teucrium occidentale*[2]
Polygonum emersum	*Typha latifolia*

[1] Relicts. [2] Invaders.

Scirpus validus is by far the most frequent of the bulrush-reed-grass dominants. This species is found in great abundance in every lake and marsh region of the sandhills as well as in smaller local spots along the streams of the region. The bulrush is found in deeper, more open water than any of the other species. The reed-grass is no less abundant but its frequency is much less than that of the bulrush and it is not found in such large stands as the latter species. The wild rice, *Zizania aquatica,* and the cat-tail are much less frequent in the sandhills than the two above-mentioned species. Nevertheless one occasionally finds extensive beds of both of the latter. The rice sometimes completely usurps shallow lakes and the tall, light-green, grassy vegetation is especially noteworthy when the large sexually divided panicles are fully developed. Again, when stands of rice, reed-grass, and bulrush alternate, a most conspicuous color differentiation results, grading from yellow-green in the wild rice through darker pea-green in the reed-grass to deep blue-green in the bulrush.

All of these species are densely social but this tendency is developed to the most exclusive extreme in *Phragmites.* The closely aggregated stems with copious leafage in this plant result in the establishment of a control that is often absolute. Within such dense stands the sunlight seldom penetrates to the water level and hence the presence of additional species is rarely noted in such places. Vigorous creeping stems anchor the plants securely, and, although these stands are sometimes exposed to powerful winds, the soil connection of the dense communities is never broken.

The bulrush ranks little below the reed-grass in density. As a matter of fact the number of erect stems may be greater in the former, but, because of the leafless nature of these stems, even the densest aggregation of bulrushes admit considerably more light than enters the reed-grass stands. The bulrush is more often seen in open association than is either of the other dominants.

The cat-tail occurs in close stands also but even with a heavy leafage the disposition of the leaves is such that the species never forms as exclusive stands as does *Phragmites.*

Wild rice, an annual non-rhizomatous species, is also seen in rather close stands, but because of its annual life cycle does not play the significant rôle in this formation peculiar to *Scirpus, Phragmites,* and *Typha.*

Throughout the region under study the bulrush exercises its common rôle as a pioneer in the invasion of water areas. This species usually encroaches upon the open water of the pond or lake by sending out scattered rhizomes which fasten themselves in the mass of débris laid down by the water-plant formation. From these first few elongating rhizomes there arises a belt of helophilous vegetation, characterized by widely scattered erect stems or more or less isolated patches of scattered individuals. Tansley has suggested (66) that "it is probable that this species can germinate from submerged seed at a considerable distance from the land." This may help explain the presence of scattered individuals or clumps far beyond the well-defined marginal belt. Beds of muck, occupied more or less scantily by submerged water-weeds, would certainly afford a prime seed bed for such species. From these outlying centers of distribution additional rhizomes are sent forth that result in the gradual increase of bottom areas held by the species and the consequent extension of the emerged portion of the association.

Wild rice invades in a similar manner although this species is

dependent solely upon seedage for its dissemination. A thin fringe of approximately equally spaced individuals of this species is more commonly seen than isolated patches or clumps. The comparatively low frequence of *Zizania* is probably due to the absence of the perennial creeping stem as well as to the fact that the fruit is so eagerly sought after by myriads of waterfowl.

The reed-grass commonly invades in solid phalanx. Widely separated individuals or clumps of this species are seldom seen in the open water. This habit is responsible for the "bank" or wall effect produced by *Phragmites* as one views these colonies from the water. Sometimes such a bank as this lies between the open water and a belt of *Scirpus* toward the shore. A very pronounced double belt of tall plants is thus produced, the two portions of which are clearly differentiated by the color of the respective species. In the deeper water, however, this sequence is usually reversed. When *Scirpus* and *Phragmites* are associated together in dense stands the latter is usually in the minority. Under these conditions of mixture the reed-grass commonly leads out into more open water along with the bulrush.

The reed canary-grass, *Phalaris arundinacea,* is a frequent member of the older portions of this association. Societies of this species are especially noticeable in midsummer after the species has ripened its seed and the whole plant has become golden yellow. The broad belts with it in dominant mixture look somewhat like fields of ripened wheat at this time. The contrast with the surrounding dark-colored members of the association is marked. So also the individuals of *Scirpus* or *Phragmites* that are scattered through the *Phalaris* areas stand out in bold contrast.

The bulrush-reed-grass association becomes considerably modified in and about the more strongly alkaline lakes. This modification may appear both in the composition and the density of the association. The reed-grass and the wild rice are greatly reduced in frequency and abundance in such habitats. Both of these species appear to be quite sensitive to an alkaline substratum above a certain concentration which has not been determined. The bulrush is not nearly so conspicuous a halophobe, but even this species, *Scirpus validus,* reveals much lower form and is less densely aggregated under the more highly concentrated conditions. The relative openness of the association is a noteworthy feature whenever the more halophilous situations are invaded. *Scirpus americanus* is the most

distinctly halophilous of all of the *Scirpi* within our limits. This species often produces extensive belts of closely grown plants which in many instances become absolutely socially exclusive. The regular position of the belts of *S. americanus* is upon a saturated beach or in the shallower water near the shore. This species sometimes mixes with *S. validus* on about equal proportions.

Typha latifolia is the least frequent of the dominant species of this association as it occurs in the sandhills. The degree of alkali-tolerance of this species appears to be low and this fact may be an important reason for its relative infrequency. This plant is, however, one of the last to give way before later invaders and so it is seen as a late relict of the marsh formation after the areas have been transformed into a later association.

Secondary species are to be found in considerable abundance between the scattered clumps or thinly distributed individuals of the dominant species of this association as we find it towards the open water. The open bays within the denser stands also reveal the presence of similar species. Along the more open water front relicts of a former association are especially common, among which *Nymphaea advena* and *Potamogeton natans* may be noted. Pelagic species such as *Lemna, Spirodela, Wolffia,* and *Azolla* are common among the erect stems of protected bays. A green or purple surface is sometimes seen in these places according as to whether the cover is composed of *Lemnaceous* species or *Azolla*. Certain algal species such as *Clathrocystis* and *Anabaena* are often of such abundance as to produce the well-known water-bloom.

The shallower open areas nearer shore are sometimes filled with *Sagittaria arifolia, S. latifolia,* or *Alisma plantago-aquatica* which occur in large stands of closely grouped individuals. Here also is found *Sparganium eurycarpum* as scattered individuals or more commonly in open aggregations. So also the less watery or older portions of the association toward the land are regularly invaded by many of the species of succeeding associations. Among these plants are *Spartina cynosuroides, Stachys palustris, Asclepias incarnata, Berula erecta, Cicuta occidentalis,* and *Teucrium occidentale.*

THE SMARTWEED ASSOCIATION

As the water recedes beneath the bulrush-reed-grass association, conditions arise that make possible the invasion of additional numbers of helophytic species. Commonly this is a slow process as

it occurs about the larger bodies of water, and the gradual development of succeeding meadow associations follows closely in the wake of the bulrush-reed-grass combination. But with the smaller lakes and ponds which are subject to rather wide fluctuations in water level, a different vegetative condition is frequently revealed. The portions of the lake or pond bottom exposed as the water recedes are often covered by a dense mass of algae and aquatic mosses and spermatophytes which linger for a time in the rich mucky substratum. Such areas often retain certain aquatic species that are able to adopt an amphibious life and these species frequently become controlling and result in the production of a vegetative type which is intermediate between the marsh proper and the wet weadow. Very frequently the initiation of this sort of control and of this association is made possible by the presence of *Polygonum amphibium* or *P. hartwrightii* as members of the pondweed association or as secondary species of the bulrush-reed-grass association. As the water-table recedes these species (*or this species*) persist while practically all the aquatic associates perish and the result is the production of a belt composed almost exclusively of the *Polygonum.*

The development of the hydro-mesophytic mode of life by these species is a fact of every-day observation. In the marshy areas of the sandhills one can trace a perfect series of changes from the typical form called *P. amphibium* through P. *hartwrightii* and finally to *P. emersum.* The first two forms, though often very different appearing plants, may commonly be collected from the same rhizome. The latter "species" is almost as variable and it seems a plain case that these three "species" are merely extreme variations that may be found arising from the *same rootstock.* The possibility of variation and successful reaction to the above great changes have provided this plant with the means of quickly unfolding a complete vegetative cover in these places. It often happens that *P. hartwrightii* or *P. amphibium* is to be found in great abundance over the lower portions of the old lake bed while a trifle higher, in a soil a little more dry and sandy, occurs a pronounced belt of *P. emersum.* Sometimes the three forms are developed in such confused variation and distribution that it is quite impossible clearly to differentiate the three as to substratum requirements. Both *P. hartwrightii* and *P. emersum* are common members of the next formation but neither is developed there to the degree that marks the above situations.

The individuals of this association are so closely grouped that

almost every other plant is excluded. The ground cover produced by the low plants is perfect in many instances. In the open areas where the *Polygonums* are found in more open aggregation the association admits a number of secondary species. Of these the commonest are *Polygonum hydropiper* and *P. persicarioides*. The latter species is sometimes seen in dense patches which alternate with the dominant species. *Rumex persicarioides* is also an occasional invader as scattered individuals or in small clusters where the association passes over directly to the rush-meadow association.

Pound and Clements have pointed out (57) certain other variations of this association (called by them the "Smartweed Formation") that are sometimes seen in the sandhills. The commonest variations are produced by the presence of *P. lapathifolium* and *P. incarnatum* sometimes associated in marshy situations, and in other cases by *P. punctatum* and *P. hydropiperoides*. The development of these various aspects is probably due to chance dissemination rather than to any significant habitat change.

Still another phase of this association is seen in the sandhills, as well as in every other region of the state, where *P. pennsylvanicum* takes exclusive possession of marshy habitats as well as relatively drier ruderal situations.

The rapid drying-up of some of the shallower lakes and ponds sometimes results in the production of rather sudden changes in edaphic conditions. These changes commonly accelerate the complete disappearance of water-plant species and tend at the same time to reduce the optimum for the marsh series, and also to favor the invasion of such areas by numerous species of later associations. A peculiar heterogeneous type of vegetation may thus prevail for a time in such shallow depressions where practically all species of the mixed population may become dominant in local patches. In the early stage of this change the aspect is strongly that of the marsh series but later, as the water-table recedes beneath the drying substratum, a strong tendency toward the meadow series appears. Instances of such a bizarre mixture of species and associations are found in nearly all of the lake centers of the region and they are always puzzling to one who has not worked out their significance.

THE STREAMSIDE MARSH ASSOCIATION

Still another expression of the marsh formation is seen along such streams as the Dismal and Loup rivers. This modification is

usually found as more or less scattered patches or slender marginal belts upon sandy soil, which, as Pound and Clements indicated (57), is commonly somewhat shaded and is constantly bathed by the waters of near-by springs or streams. The appearance of this association is thus seen to be quite different from the broad belts or extensive tracts of low valley commonly controlled by the bulrush-reed-grass association which covers hundreds of acres of the sandhill lowlands.

I have chosen to unite in this association the "spring marsh type," "characteristic of the sandy marshes about the sources of streams," and the "spring brook type" of the "wet sandy margins of spring branches" of the above authors, because after an extensive reconnaissance of the region these two "types" appear to be but slight modifications of a single unit that may be properly designated as an association.

As might be expected from the close relationship of this association to the other marsh associations, and to the earlier members of the meadow formation, it has been found that in addition to a number of species quite distinctive of the streamside marsh there are many species from these related associations that wander in and often become locally dominant.

Beneath the shade furnished by a more or less well-developed arborescent cover we find the conditions which really make desirable the delimitation of this association. In the saturated soil of such situations we often find such species as *Impatiens biflora, Epilobium lineare,* and *E. adenocaulon* associated with some of the species already noted in the formation. The touch-me-not dominates wide areas in such sites and is to be considered the greatest modifying factor of the marsh aspect as represented in this association. This plant is more commonly a pronounced mesophyte in other regions, but here it partakes strongly of the helophilous condition. Furthermore, the dense aggregation that characterizes this species as a mesophyte is not the commonest aspect of its development in this association. The aspect here is much more open so that one finds mixed with the *Impatiens* such species as *Helenium autumnale, Rumex britannica, Eupatorium perfoliatum, E. purpureum, Mimulus jamesii,* and *Berula erecta.* The two latter species sometimes develop a marked secondary layer beneath an open touch-me-not cover. *Helenium* is often seen in dense clusters. *Bidens trichosperma, B. levis, B. frondosa, Alsine longifolia,* and *Homalocenchrus*

oryzoides are common members of this association as it is seen in linear form near streams. Some of the species that have already been noted for the marsh are more or less common as straggling communities in this association. Thus *Scirpus validus, S. americanus, Phragmites,* and *Typha* are all frequently seen as tufts or narrow patches either in pure or mixed stands along all of the streams of the region. Numerous additional sedges become locally abundant. Tufted species of *Carex* such as *C. gravida, C. festucacea, C. stipata,* and *C. hystricina,* are especially common in such places.

The Meadow Formation

The earliest aspect of the meadow formation is seen in the form of a wet meadow, as a rule closely following the bulrush-reed-grass association of the previous formation. Occasionally the smartweed association or the streamside marsh variations lie between the meadow and the more aquatic associations. The wet meadow is usually intermediate in position and development between marshes and meadows proper. Where, as along streams, the marsh formation is developed in the form of straggling bits or in narrow marginal belts, this formation is often conspicuous as alternating patches that occupy slightly higher levels but still with a soil that is very wet and soggy for the most of the season.

The lowest of the meadow associations, namely the rush-sedge wet meadow association, because of a slightly more elevated position occupies a sandy substratum with a much lower soil-moisture content than is characteristic of the marsh, although during wet seasons this difference becomes much less. Quite naturally this and the previous formation are not separated by a definite boundary line, but because of a very gradual change in edaphic conditions a transition belt is usually noted within which the one formation loses its identity and the other makes its appearance. Such belted transition areas are frequently of considerable breadth and their floristic character partakes of the typically developed formations lying on either side. On the other hand a more abrupt change is brought about where the pond or lake is bordered by a distinct bank a few feet in height. Under such circumstances the wet meadow species may be totally absent, while the other meadow forms approach the edge of the low rim which constitutes at the same time the outer boundary of the marsh formation. Abrupt topographic transitions are thus seen

to result in very sharply delimiting these closely related formations.

The meadow formation in its various aspects is often very highly developed as a belt, or a series of belts, about lakes and ponds and in the lower valleys in many parts of the sandhills. Neighboring marshes are sometimes connected by a stretch of slightly higher land covered by meadow associations.

THE RUSH-SEDGE WET MEADOW ASSOCIATION

The earliest stage in the development of meadow vegetation and one of the most common types of this formation throughout its range in the sandhills is the rush-sedge wet meadow association. From their sub-paludose nature wet meadows are characterized by the presence of sedges and sedgelike plants of the genus *Juncus,* commonly termed *rushes.* Some such meadows contain little in addition to sedges while in other places the *Junci* are dominant. Very commonly the two groups occur in various mixtures. Many other moisture-loving species become especially abundant as secondary species wherever the association is more or less open. The extremely rich floristic composition of this association is indicated in the lists that follow.

Composition of the Rush-Sedge Association

DOMINANT SPECIES

Carex trichocarpa
Eleocharis acicularis
Eleocharis acuminata
Eleocharis glaucescens
Eleocharis palustris
Juncus balticus
Juncus marginatus
Juncus nodosus
Juncus tenuis
Juncus torreyi
Scirpus americanus

PRINCIPAL SPECIES

Agrostis hyemalis
Caltha palustris
Campanula aparinoides
Distichlis spicata
Dodocatheon meadia
Halerpestes cymbalaria
Juncus longistylis
Lilium umbellatum
Lotus americanus
Lythrum alatum
Panicularia americana
Panicularia nervata
Plantago eriopoda
Spartina cynosuroides
Steironema ciliatum
Strophostyles pauciflora
Triglochin maritima

SECONDARY SPECIES

Agrostis alba
Alopecurus aristulatus
Asclepias incarnata[1]
Calamagrostis neglecta
Carex festucacea
Carex gravida
Carex hystricina
Carex lanuginosa
Carex marcida
Carex nebraskensis
Carex scoparia
Carex stipata
Carex stricta
Catabrosa aquatica
Cicuta occidentalis
Crepis runcinata
Cyperus inflexus
Epilobium lineare
Eriophorum gracile
Galium trifidum
Galium triflorum
Gentiana andrewsii
Gentiana puberula
Gerardia besseyana
Gratiola virginiana
Habenaria leucophaea
Helianthus tuberosus
Hordeum jubatum
Hypericum majus
Hypericum virginicum
Hypoxis hirsuta
Ibidium cernuum
Ibidium strictum
Leptorchis loeselii
Lobelia spicata
Lobelia syphilitica
Lycopus lucidus
Mentha canadensis
Menyanthes trifoliata
Naumbergia thyrsiflora
Phalaris arundinacea[1]
Polygonum emersum
Polygonum hartwrightii[1]
Potentilla paradoxa
Prunella vulgaris
Ranunculus sceleratus
Rumex britannica[1]
Sagittaria arifolia[1]
Scirpus pallidus
Scutellaria galericulata
Stachys palustris
Teucrium occidentale
Typha latifolia[1]

[1] Relicts.

The soil occupied by this association is usually very wet, and in the early spring or summer surface water to a varying depth may be encountered in many portions of the association. This condition mostly disappears with the coming of summer but even then the dark sandy soil with considerable organic residue may yield water by the ordinary pressure of the hand or by tamping with the feet. Since in many places the association occupies a substratum that was at one time lake bed, the surface soil is liable to be exceedingly mucky and to reveal quantities of the remains of various aquatic plants and animals. The water-content control is seen best whenever the belted aspect of the association appears along gently sloping

shores. Over the more undulating flats from which surface water has permanently disappeared, the association usually becomes more patchy by the invasion of species from other associations and by a soil-moisture or alkali differentiation among the regular members of the association. This latter condition often results in breaking up the characteristic belted condition and in the production of a patchwork in which locally dominant species alternate in a great variety of combinations. With the drying days of summer the surface water disappears, and many previously dormant roots and rhizomes send forth myriads of individuals of the numerous principal and secondary species, and for a time at least the uniform dark-green grassy nature of the association is notably interrupted by the blooming of these species.

The presence of the *Junci*, species of *Eleocharis*, and other sedges in close aggregations, are to be regarded as the typical expressions of this association. These often occur in mixture as well as in almost pure stands which cover the ground quite to the exclusion of all other species; *Eleocharis palustris*, ranging from the marsh formation to its greatest expression here, is often seen in extensive stands of such density as to completely, and for a long time, prevent invasion. The number of individual stems in a square yard under these conditions is astounding.

The other typical aspect of the association is seen more commonly when the dominant species occur in a much more open stand, thus making easily possible the incoming of many additional species. This more open association might indeed be classified as another association or sub-association if it were not for the fact, that, taking the vegetative season as a whole, the sedges and rushes are controlling. Aside from this fact the most noteworthy structural character of the association is the presence, at certain seasons of the year, of various social principal and secondary species in such abundance as to mask completely the dominants in localized areas. These species sometimes take the form of remarkably well-developed layered societies. The most frequent and conspicuous examples of this kind of distribution occur with *Campanula aparinoides, Mentha canadensis, Lotus americanus, Steironema ciliatum, Naumbergia thyrsiflora, Caltha palustris, Menyanthes trifoliata, Gerardia besseyana, Lythrum alatum, Lilium umbellatum,* and *Halerpestes cymbalaria.* Less abundant social species of wide distribution are *Lycopus lucidus,*

Galium trifidum, G. triflorum, Teucrium occidentale, Stachys palustris, and *Scutellaria galericulata.*

The more alkaline situations frequently show a broad belt or scattered patches of *Scirpus americanus* inserted between the marsh formation and this association. This plant is often as exclusive as *Eleocharis palustris.* Very commonly also this species becomes dominant in depressions well within this association.

Clearly defined societies of the halophilous *Triglochin maritima* and *Plantago eriopoda* are common over low, flat divides between alkaline lakes and ponds in many of the wet valleys. The former species often reaches such a degree of abundance as to produce an extremely tenacious sod in a soil that is so alkaline as to show crystallized material on the surface. The common salt grass, *Distichlis spicata,* is also commonly found in similar situations covering wide expanses with its close sod to the exclusion of all other species of plants. A peculiar tall, slender, and diffuse form of the salt grass was found in stands of *Scirpus americanus* and other taller members of this association. This form is so noticeably different from the usual habit of the species as to appear as an entirely different species upon first sight.

A contrast effect produced by a species of this association must be mentioned in closing. *Agrostis hyemalis* is a frequent and abundant member of this association which often exhibits a very perfectly belted type of distribution. These belts are conspicuous about many of the lakes. The regular position of the belt is immediately back of the marsh formation where there is a rather short transition to a little higher, harder land on the shore. The inner portion of the belt is usually very clean cut, but toward the uplands the individuals gradually dwindle away until the belt is lost in some other aspect of the association. These belts, which are sometimes 30 feet or more broad, are especially conspicuous because of the stretches of densely tangled, light-purplish to bright straw-colored panicles which contrast vividly against the dark green background.

THE WATER HEMLOCK ASSOCIATION

This is essentially the "water hemlock formation" of Pound and Clements. In the regions of ponds, lakes, marshes, and wet meadows, and locally also along some of the stream courses, *Cicuta occidentalis* is sometimes developed to a decidedly controlling degree. The plants of this species tower above the many lower wet

meadow forms, thus in dense association completely dominating wide expanses that are otherwise in reality of the wet meadow type. The most of the characteristic wet meadow species are lacking in these areas however.

Composition of the Water Hemlock Association

DOMINANT SPECIES

Asclepias incarnata	*Phalaris arundinacea*
Cicuta occidentalis	*Scirpus atrovirens*

ASSOCIATED SPECIES OF LESS ABUNDANCE

Agrostis hyemalis	*Mimulus jamesii*
Berula erecta	*Scirpus americanus*
Cicuta bulbifera	*Scutellaria galericulata*
Halerpestes cymbalaria	*Spartina cynosuroides*
Hordeum jubatum	*Stachys palustris*
Lythrum alatum	*Teucrium occidentale*

The close relationship between this and the last association is seen from a comparison of species lists from the two. The above enumerated species are those that are most common in this association and they are all found in the previous association, but as a rule in greater abundance in the present association.

This association is a noteworthy feature in the associational contrast of the lowlands during late July when the water hemlock is in bloom. The tall, scantily leaved, slender stems with their numerous, large, convex umbels of white flowers constitute, with the darker greens, a background against which the rose-colored flower clusters of *Asclepias incarnata* contrast remarkably.

Although the usual relation is more clearly with the wet meadow association, the presence of members of the marsh series in the lower situations indicates a rank about parallel with the rush-sedge wet meadow association. So also in the drier sites certain typical meadow plants are found invading the water hemlock areas, and here the association bears an unmistakable close relationship to the hay meadow association to be discussed in the following pages. The hemlock is frequently seen as relicts in lower portions of the hay meadows. It seems therefore in general that this association is a hydro-mesophilous one with a more decided tendency toward mesophytism than the previous association, and that it should be linked

with the meadow formation rather than with the marsh series as proposed in the Phytogeography of Nebraska.

THE FERN MEADOW ASSOCIATION

Still another modification of the typical wet meadow conditions which regularly lie between marshes and meadows is the fern meadow. This widespread and oddly constructed type is a proper subdivision of the meadow formation with a distinct hydrophilous inclination as possessed also by the water hemlock association. With the work that has been done upon these two associations it is impossible to say which is the more mesophytic and which the more hydrophytic. The fern meadows are seen in maximum expression in the lake regions of Cherry County but have also been noted in less noticeable degree in other meadow and lake centers and as local patches along all of the streams of the sandhills.

Composition of the Fern Meadow Association

DOMINANT SPECIES

Dryopteris thelypteris	*Onoclea sensibilis*

ASSOCIATED SPECIES

Calamagrostis neglecta	*Mentha canadensis*
Campanula aparinoides	*Naumbergia thyrsiflora*
Galium trifidum	*Stachys palustris*
Galium triflorum	*Teucrium occidentale*
Lotus americanus	

The two ferns are absolutely controlling. *Dryopteris* especially is often seen in such density as not only to exclude all other plants but to produce a ground cover about a half yard in height that is so tangled that walking is difficult over such areas. However, it is more commonly the case that the ferns are sufficiently open to admit of a number of secondary species such as the two *Galiums* noted above and the galium-like *Campanula aparinoides*. These harsh, sprawling, clinging stems tangled with the ferns produce a very troublesome cover.

The association usually occupies rich loamy soil and, in regions where cattle run over the wet meadows during times of high water-content of the soil, is broken up into innumerable hummocks with intermediate depressions about eighteen inches in depth which some-

times reach to the water table. An average diameter of these more or less cylindrical holes is about twenty inches and that of the soil columns topped with plants is about the same. This condition may result in almost any part of the wet meadow with firm soil and, as might be imagined, introduces a surface character often hidden by the vegetation, that becomes dangerous to animals that are pastured in such places.

The relation of the two ferns to light is quite different. *Dryopteris* is rarely seen within the shadier portions of the wet meadows or in the shade of taller associations, but *Onoclea* is a frequent member not only of the more shaded portions of this association, but is also seen in the more open woodlands near the streams of the region. The association becomes somewhat mottled when the two dominant species control alternating areas.

THE HAY MEADOW ASSOCIATION

The many broad valleys of the northern half of the sandhill region, and less so also the valleys of the southern portion, reveal the presence of wide expanses of flat, but relatively dry soil above that of all of the lowland associations thus far considered. The area of such land varies naturally with every valley. Some narrow valleys with finger lakes show practically no flat land between the marsh or wet meadows and the bunch-grass upland. In many cases, however, much of the valley floor lies between the wet meadows and the first hills. This type of land is covered in the main by grasses and other plants which are annually mowed by ranchmen along with parts of the wetter meadow for hay. Thousands of tons of valuable product are thus derived from the lowlands to supplement the upland forage crop which is very seldom cut for hay.

The soil of the association is usually a fine sandy loam with considerable humus and very excellent water-content relations as is shown by the fact that this sort of land, when broken up and put to agricultural uses, produces goodly yields of various field and garden crops. The water-table lies but a short distance beneath the surface. This fact has not been properly appreciated by homesteaders and ranchmen who have attempted to grow deep-rooted crops such as alfalfa upon this land. Commonly these persons have witnessed the "drowning-out" of a crop that might be grown on higher situations even in the "arid sandhills." Surface water is usually present over the lower portions of this association where it joins with the

rush-sedge wet meadow association, or, in the absence of this, where it meets the marsh formation.

The usual position of the association in relation to other vegetation groups has been indicated as between the xerophilous upland associations and some one of the lowland associations already described. Toward the uplands the hay meadow very soon fuses with, and is lost in, one of the typical grass associations of the hills, most commonly the bunch-grass association. In the opposite direction the hay meadows may give way at once or through a less conspicuous transitional belt to either rush-sedge wet meadow association or to some aspect of the marsh formation.

Naturally many of the typical meadow grasses are to be found here, and with them numerous herbaceous associates of meadow associations farther eastward as well as some of those species more or less common in the outer stretches of the above meadow associations, as they occur within our sandhills. This association is somewhat like the "long-stemmed" grass formation of Pound and Clements. It includes the most of Rydberg's (58) "dry valley" and "meadow" species.

Composition of the Hay Meadow Association

DOMINANT SPECIES

Agropyron pseudorepens	*Elymus canadensis*
Agropyron smithii	*Koeleria cristata*
Agropyron tenerum	*Panicum virgatum*
Agropyron violaceum	*Spartina cynosuroides*
Agrostis alba	*Stipa comata*
Andropogon furcatus	*Stipa spartea*
Calamagrostis neglecta	

ASSOCIATED SPECIES OF VARYING RANK

Amorpha canescens	*Drymocallis arguta*
Andropogon scoparius	*Eatonia obtusata*
Anemone cylindrica	*Equisetum laevigatum*
Beckmannia erucaeformis	*Equisetum pratense*
Boltonia asteroides	*Erigeron bellidiastrum*
Bouteloua curtipendula[2]	*Euthamia graminifolia*
Calamovilfa longifolia	*Fragaria virginiana*
Cicuta occidentalis[1]	*Helianthus subrhomboideus*[2]
Delphinium albescens	*Lacinaria spicata*

Linum sulcatum
Lotus americanus[1]
Lycopus lucidus
Lythrum alatum[1]
Meibomia canadensis
Muhlenbergia racemosa
Naumbergia thyrsiflora[1]
Panicum dichotomum
Panicum implicatum
Panicum scribnerianum
Psoralea argophylla
Psoralea tenuiflora
Ratibida columnaris
Rudbeckia hirta
Silene antirrhina
Solidago canadensis
Solidago rigida
Solidago serotina
Sorghastrum avenaceum
Thalictrum purpurascens
Viola obliqua

[1] Relicts.

[2] Invaders.

I have chosen to call this type the hay meadow association because of its very important economic relation. It must not be supposed, however, that all of the hay of the region is made from this association. A considerable quantity of this product is harvested from certain upland associations, and, indeed, especially during the drier years, much of the area occupied by the rush-sedge wet meadow association is cut over and made to yield much valuable hay. The latter association, as a rule, covers a substratum too wet to permit of hay-making operations with the average rainfall, but, although the hay is somewhat inferior, it becomes of much value in times of drought when the usual meadows are "short."

Because of the large number of grasses in these meadows that reveal little or no striking alternation, the association exhibits a rather homogeneous structure. As Pound and Clements state the meadow associations are typically *closed* and the dominant plants are relatively long-stemmed, sod-forming species. This condition stands in marked contrast to that seen over the bunch-grass uplands. A uniformly developed grassy cover, in which the above dominant species compose a layer varying in height from one-half yard to one and one-half yards, revealing beneath the presence of numerous principal and secondary species of showy natures, is the typical expression of the hay meadows as found in the sandhill region.

The dominant species and their associates are markedly reduced in number and abundance as the meadow becomes higher and drier and approaches those conditions known as "dry valleys" in which short-grasses are not infrequently found. The great number of mesophytic species lag behind as these situations are reached, and

the few more xerophytic grasses and herbaceous interstitials become more prominent.

The development of the controlling or secondary species to a condition of local dominance is seen in a few instances. Thus *Spartina cynosuroides* exercises an almost exclusively dominant influence over small areas in swales and other slight depressions. *Eatonia obtusata, Calamagrostis neglecta,* and *Elymus canadensis* often control small stretches of higher land at certain seasons.

The species that are most frequent inclusions of the association as members of a secondary layer are the copious *Rudbeckia hirta* and *Ratibida columnaris* which, with their myriads of yellow heads, often transform the drier stretches of the hay meadows into perfect fields of golden bloom that are visible for miles. Again the ubiquitous lowland socials such as *Mentha canadensis, Naumbergia thyrsiflora,* and *Steironema ciliatum* wander from the moister associations and develop low, strictly bounded aggregates in lower, moister situations that occur in many places throughout the hay meadows. The colonial *Psoralea argophylla* invades in a similar manner the more open and drier portions of the association. The polydemic, *Lotus americana,* forms here, as well as in other associations, very dense communities that add considerable value to the native hay. *Linum sulcatum* is a frequent species of the hay meadows which occasionally becomes sufficiently abundant and aggregated to be very conspicuous. This tendency stands in marked contrast to the habits of the upland flax, *L. rigidum.*

When such meadows as these are pastured to too great a degree many of the valuable species become greatly reduced or killed out entirely and then some of the secondary species with a ruderal tendency become strongly emphasized. As the soil becomes tramped and exposed by grazing animals, such species as *Solidago rigida, Euthamia graminifolia,* and even *Cleome serrulata* come in and form large dense patches. Occasionally it happens that the drier portions of the hay meadows are pastured along with the uplands and with the tramping-out of the meadow species an area is exposed to strong wind action, and a great "blow plain" is produced which then requires the presence of *Redfieldia* or *Psoralea lanceolata* to correct. This condition is particularly liable to occur in places where stock continually cross a portion of the meadow on their way to water.

The hay meadow association presents the nearest approach to the typical sod associations of the prairie-grass formation to be

found within the sandhill region. With a little higher and drier soil the association would probably be transformed either into the bunch-grass association if the soil is especially sandy, or, if the soil is harder and less sandy, into the spear-grass association. The change to the grama-buffalo-grass or wire-grass transition associations is also possible in certain portions of the hills, although the relatively mesophytic association appears to be the more probable culminating point on the harder bottom land throughout the region.

THE WILLOW THICKET ASSOCIATION

The hay meadows and wet meadows are often strikingly modified by the presence of a chaparral type of vegetation in which *Salix longifolia* is the dominant plant. Extensive tracts of wet meadow and lower stretches of hay meadows are broken by the presence of round-topped bushy plants varying in height from 6 to 10 feet. Sometimes the willows are often disposed in the form of a belt lying along the outer margin of the marsh formation, thus occupying a position with which the rush-sedge wet meadow is correlated. This belted appearance is a most pronounced feature of such meadows when viewed from some vantage point in the uplands. The belts frequently become discontinuous and then the association takes the form of more or less isolated patches or islands dotted over the drying meadow.

The much-branched, bushy form of the controlling species with its relatively high tolerance results in the production of dense crowns which produce shade too deep for most of the lower wet meadow herbs. A few species, such as *Campanula aparinoides, Galium triflorum, G. trifidum,* and *Scutellaria galericulata,* succeed in populating the less open intervals between the willow clumps. *Amorpha fruticosa,* a woody species of about the same height as the willow, is occasionally seen in mixture with the willow, but seldom, if ever, becomes sufficiently abundant to dominate the scrub. This species is much less tolerant than the willow and hence it usually occurs in the open portion of the association and as scattered individuals along its margin. Relicts of the marsh formation are commonly present among the willows as scattered tufts or single individuals, while in the drier situations, where the willows become open, many species of the hay meadows invade and completely dominate the interspaces beyond the shade of the willows.

This asociation is doubtless an extension and a modification of

the *Salix-Amorpha* combination which has already been discussed under woodland vegetation. The group is not to be considered as playing a significant rôle in the lowland successions which culminate in the hay meadow association, but rather as an intruding type which here and there takes a conspicuous part in the vegetative cover of certain meadows.

RUDERAL VEGETATION

There are a number of plants that are regularly found in and about waste places. To this number may be added others that are regular members of certain of the above plant associations which now and then reveal a decided ruderal tendency. The following list includes the commoner plants of this nature.

RUDERAL SPECIES

Amaranthus graecizans
Amaranthus hybridus
Amaranthus retroflexus
Amaranthus torreyi
Ambrosia artemisiaefolia
Argemone intermedia
Bromus brizaeformis
Bromus tectorum
Cannabis sativa
Cassia chamaecrista
Chaetochloa glauca
Chaetochloa viridis
Chenopodium album
Chenopodium hybridum
Cleome serrulata
Cryptanthe fendleri
Cycloloma atriplicifolium
Dyssodia papposa
Echinochloa crus-galli
Eragrostis pectinacea
Glycyrrhiza lepidota
Helianthus petiolaris
Hordeum jubatum
Hordeum pusillum
Iva xanthifolia
Lactuca canadensis
Lactuca pulchella
Lepideum apetalum
Leptilon canadense
Malva rotundifolia
Melilotus alba
Melilotus officinalis
Munroa squarrosa
Oxalis stricta
Physalis heterophylla
Polygonum aviculare
Polygonum convolvulus
Rumex venosus
Salsola tragus
Solanum rostratum
Verbena stricta

The species of *Amaranthus, Ambrosia,* the *Chaetochloas, Chenopodium album, Cycloloma, Hordeum jubatum, Helianthus petiolaris,* the *Lactucas, Polygonums, Salsola,* and *Solanum rostratum* are frequent and abundant in old fields and gardens. These species

are especially common about old "claims" where small tracts of land were broken up and then allowed to "go back." Such plants are especially common as initial species in the "weed stage" which always precedes the invasion of certain grasses and the reversion of the broken area to one of the grassland associations. The ruderal, *Hordeum jubatum*, often completely dominates stretches of plowed ground in valleys and meadows where the stands become especially conspicuous in midsummer. *Cycloloma* and *Amaranthus graecizans* are very common old field, fire guard, and garden species of the tumble-weed character. I have seen old fields of several acres in extent covered by the scattered, hemispherical plants of *Cycloloma*, many of which were more than a yard in diameter. The Russian thistle, *Salsola tragus*, is also common in such places. Dense stands of this plant on "new land" are sometimes cut for hay when young and succulent. *Cleome serrulata* is especially common in close stands about and within old feed yards and corrals. The nightshade, *Solanum rostratum*, as also *Ambrosia* and *Argemone*, are most frequently seen in similar modified situations. *Munroa squarrosa*, *Cryptanthe fendleri*, and *Plantago purshii* are common abundant inhabitants of prairie-dog "towns." Common roadside plants are *Cassia chamaecrista*, *Verbena stricta*, *Dyssodia papposa*, and *Melilotus* especially, as in valleys, where the soil is much more compact than up in the hills. The hemp is occasionally seen in characteristic stands about stock yards, dump heaps, and similar waste places. The sunflower, *Helianthus petiolaris*, and the rose dock, *Rumex venosus*, are among the most noticeable species with a ruderal tendency. The former species often occurs in very dense stands about one-half yard in height over broad fields or in the form of dark green belts following fire guards over the hills. The dock occurs in similar habitats but the appearance is very different because of the low, sprawling plants and the large clusters of very conspicuous, rose-colored to dark red, winged fruits. This feature becomes especially pronounced when the species occurs in extensive stands over relatively bare stretches of the light-colored sand.

SUMMARY OF SUCCESSIONS

We have seen that the vegetation of the sandhills is peculiarly grassy, hence any significant alterations in the vegetative cover of this region will be most typically mirrored in the great stretches of

grassland. The woodland vegetation of the region is derived, as I have shown, from two widely separated forest centers and appears to play an unimportant rôle in the characteristic plant successions as they occur within the region under study. There is evidence in some quarters of a slight displacement of grassy associations by woodland forms, but on the whole this tendency is so slight that it may be passed with mere notice. There is every evidence that the uplands, as well as the most of the lowlands, will never become completely occupied by the eastern type of woodland, at any rate as long as the present control remains. Furthermore, it appears that the frontier of a western forest complex represented by *Pinus ponderosa scopulorum* is slowly losing ground within this region.

All of the associations (except the woodlands) as delimited above are stages, or closely related to stages, in one of two great successional series. One of these begins with the appearance of certain plants in blow-outs or similar situations leading to the production of relatively stable conditions and to the invasion by other slightly less wind-tolerant plants and a still further decrease in blow-out dynamism, and, eventually, with the coming of additional wind-resistant species, ends, at least temporarily, in the establishment of the bunch-grass association. The other, beginning when the first water-plants make their appearance in the ponds and lakes of the region, culminates, at least temporarily, in the establishment of the hay meadow association.

The progress of the first series has been described at some length in connection with the prairie-grass and short-grass formations. The first stage in the regular succession is always represented by the blow-out association which, by means of a number of phases which can not be satisfactorily delimited, gradually passes over into the bunch-grass association. This association is to be regarded as the temporary climax in the upland cycle. The association, because of the extreme rigors of its habitat and the very slowly changing substratum, appears to represent a long persistent type of vegetation and at the same time to pass over, under certain conditions, to a more typically sodded prairie-grass or possibly short-grass cover.

While the bunch-grass habit of the dominant species appears to be the perfect solution of these particular environic conditions, yet the frequency and abundance of many interstitial species with a strong relationship to the more extensive prairie-grass types farther

eastward, constitutes a prophetic index of the possible culmination of the upland series. Furthermore, the encroachment of the spear-grass association upon the domain of the bunch-grasses is another indication, in the form of a connecting link, of the most evident relationship between the bunch-grass association and the other types of vegetation represented in the great prairie province. The ready adaptability of *Stipa comata* to a substratum slightly more stable than that occupied by the bunch-grasses, and its ability in following with the sod-forming habit as the soil becomes more stable and harder, brings forth the suggestion that the spear-grass association is probably destined eventually to supplant the bunch-grasses over the greater portion of the sandhills region. The pathway may thus be prepared for the occupation of the region by some of the more distinctly sodded associations of the prairie-grass formation. Evidences of such an intermediate position held by the spear grasses are especially strong in the sub-sandhills of the northern and eastern portions of the region.

Toward the drier western limits of the region other possibilities are presented. Here the wire-grass transition association is seen grading on one hand into bunch-grass land and on the other merging upon the more flat clayey land into the short-grass formation. The evidence, therefore, appears to favor the conclusion that at least in some cases the bunch-grasses may be regularly succeeded by a short-grass cover. This is taking place on the western border of the hills and in some of the less sandy outlying sandhill areas as in Chase and Dundy counties.

Since it is an apparently unquestionable fact (Shantz 60) that the short-grass formation is correlated especially with a relatively low rainfall and low available soil-moisture as compared with the prairie-grass formation, it may be that the area of short-grass land is to become greater in these particular portions of the sandhills. At any rate the short-grasses have come into complete control of sandhill areas in Chase and Dundy counties and *Andropogon scoparius* remains merely in the form of relicts.

In short, the present state of rather unstable climatic and edaphic equilibrium which exists along this semiarid short-grass and prairie-grass frontier appears to favor the short grasses, while farther eastward a higher normal precipitation and a higher available soil-moisture in a sandier soil and at greater depths, makes possible the continued supremacy of the prairie grasses and their

many deep-rooted associates. Such are the conditions that mark the tension line between these two broad types of grassland.

Disturbing factors sometimes interrupt the course of a regular vegetative cycle. The influence of grazing is especially noticeable in the sandhills during these later years when the range has been fenced to a degree that was unknown to the older cattlemen. A comparison of the vegetation on opposite sides of a fence often pictures in a vivid manner the destructive effect of too severe pasturage. The degree of denudation produced by the stock is sometimes so great as to bring about a reversion to blow-out conditions and the subsequent development of the plant association characteristic of such conditions. Prairie fires often initiate the same retrogressive cycle. Grazing and fire sometimes combine in bringing about the subjugation of the bunch-grasses or other grassy associations and the reëstablishment of the blow-out association. Working thus together or separately these forces often eradicate the great majority of the deeper-rooted secondary species of the sandy uplands. During the earlier stages of bunch-grass disintegration *Muhlenbergia pungens* is liable to become very abundant and controlling over wide areas. This species forms an association at such times that is almost as pure and exclusive as the short-grass cover of dry, hard soils. The Muhlenbergia association may appear as a stage interpolated between the blow-out association proper and the bunch-grass association proper, although quite naturally at one time it may partake more especially of the nature of the one association and at another time the other association. There is thus some evidence to indicate that perhaps *Muhlenbergia pungens* once played a significant rôle in upland successions which has, however, now all but completely disappeared.

No evidence has been gathered which indicates that the destruction of the bunch-grass association by either fire or grazing animals ever results in the establishment of a "pure short grass cover" as Shantz records (60) for eastern Colorado. The typical bunch-grass land in our sandhills is far too sandy and exposed to too great wind action to permit of this succession. The regular process in this connection is, as has been shown, a reversion to the blow-out association and the probable subsequent reëstablishment of the bunch-grass association in a number of years if the denuding influences are removed.

When bunch-grass land is "broken" one of two different prob-

abilities are invited. If the site is exposed to wind action the almost invariable consequence is the immediate generation of blow-out phenomena. But if wind action is not so severe, breaking regularly leads to the early establishment of the various ruderal combinations. These "weed stages" are most commonly represented by the species noted under the discussion of the ruderal vegetation of the region. Through a series of changes which have not been thoroughly studied the ruderals eventually yield their position to the bunch-grasses.

The spear-grass association may also be caused to revert to the blow-out association after breaking, or such areas may be dominated for a number of years by ruderal mixtures after which the bunch-grasses invade and later the spear-grass again appears. When valley land with either spear-grass or bunch-grass vegetation is broken *Hordeum jubatum* often comes in in great abundance so that such areas are very conspicuous. This same "weedy grass" also invades, along with *Cycloloma, Amaranthus graecizans,* and *Salsola,* areas of the wire-grass transition association after breaking.

The lowland successional series begins with the aquatic pond-weed association and follows more or less in correlation with the developing humus complex through the water lily association to the marsh formation. From this point we have traced the development and structure of the bulrush-reed-grass and smartweed associations with their common variations as they are correlated especially with a decrease in soil-moisture and a receding water-table. As the substratum becomes progressively harder and drier we have witnessed the development of the meadow formation with its rush-sedge wet meadow and other associates, finally leading to the establishment of that extensive and valuable type which I have called the hay meadow association. Rarely is this series interrupted through the operation of the forces that so often affect the regular course of upland successions. The hay meadow appears to mark the culmination of this particular series, yet, while the evidence is not as complete as it should be, conditions have been observed which indicate that this type should be regarded as a "temporary climax."

Certain evidences are prophetic of a still further development from the typical meadow structure to that possessed by one of the prairie-grass associations. Indications of such a possible transition have been observed where the hay meadows and certain prairie associations have become intermingled. Modifications of the hay

meadows arising from invasion by *Stipa* and *Agropyron* have been observed in a number of places. These facts lead to the tentative conclusion that the final vegetative cover of the sandhills may be composed of one or more of the *sod-forming prairie-grass* associations and the bunch-grasses will remain as relicts upon the more extremely xerophilous, sandy situations.

Thus it appears from the data collected during the preliminary investigation of the structure and development of the vegetation of the sandhills of Nebraska that we have here two prominent successional series. One of these originates under the peculiar xerophilous environment of a sand dune complex, while the other begins in an extremely hydrophilous situation. And furthermore, as a tentative conclusion, it appears that each of these series progresses toward, and will ultimately culminate in, the relatively mesophytic sod-forming associations of the prairie-grass formation.

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Fig 1. A general view of the sandhills in a region of short valleys and "pockets." The vegetation here is bunch-grass association. Over-grazed.

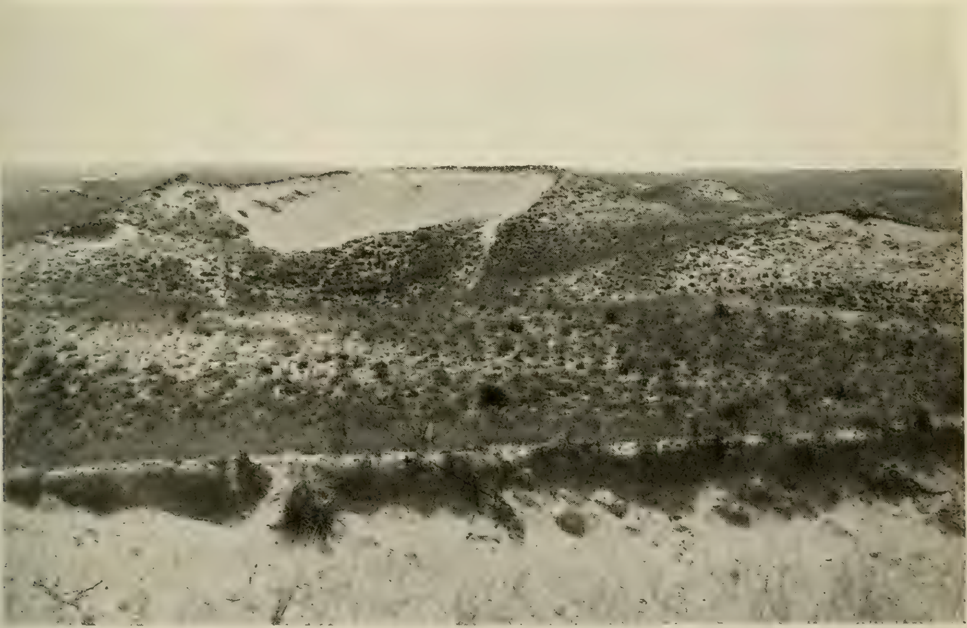


Fig. 2. The same kind of a region with active blow-outs. The prominent ridge in the foreground is the rim of a large blow-out similar to the one in the background.

PLATE XXVI

Fig. 1. The underlying rock with the veneer of sandhills above. The stream is the Middle Loup River in Thomas County.

Fig. 2. The sand is very commonly stratified. This shows a series of sand layers as they are often exposed on the bare sides of blow-outs.

PLATE XXVII

Fig. 1. The *Yucca* in fruit. In over-grazed areas all of the flowers of this species are eaten by stock.

Fig. 2. *Ceanothus ovatus pubescens* in characteristic distribution over the bunch-grass uplands.

PLATE XXVIII

Fig. 1. The sand cherry, *Prunus besseyi,* one of the common gregarious species of the uplands.

Fig. 2. *Ipomoea leptophylla,* the big-rooted bush morning glory, is very common especially westward.

PLATE XXIX

Fig. 1. The rim of an active blow-out showing the fringe of uprooted plants.

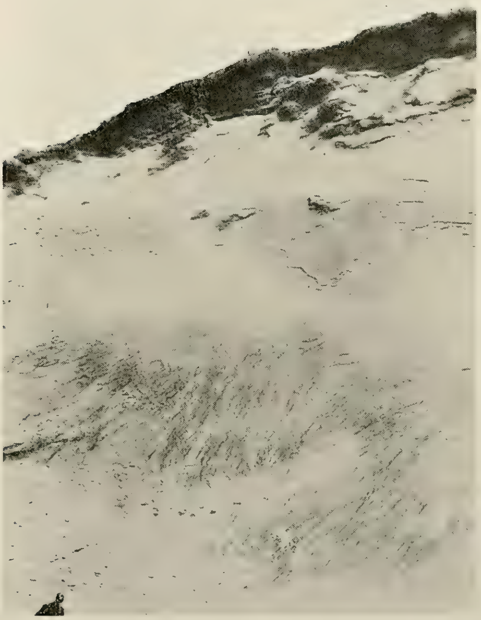


Fig. 2. *Redfieldia flexuosa* spreading over the side of a large active blow-out.

PLATE XXX

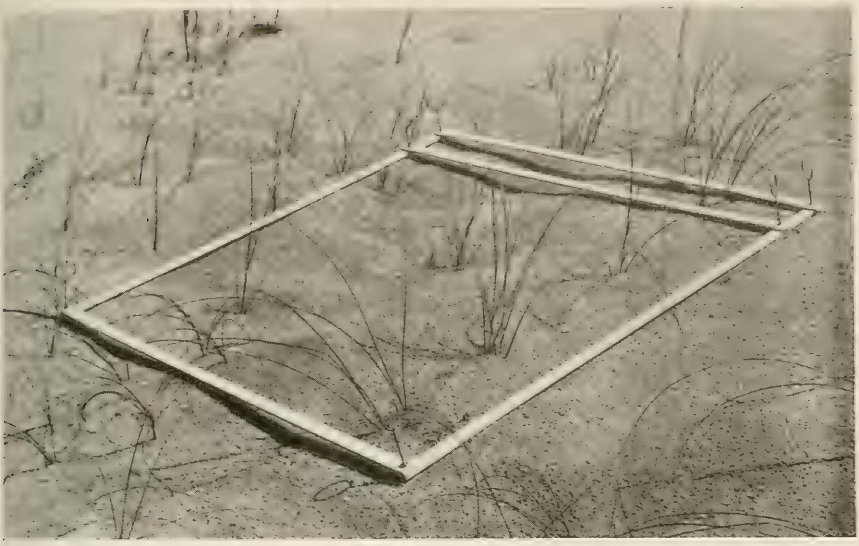


Fig. 1. A meter quadrat in a blow-out showing the distribution of *Redfieldia* during early stabilization.

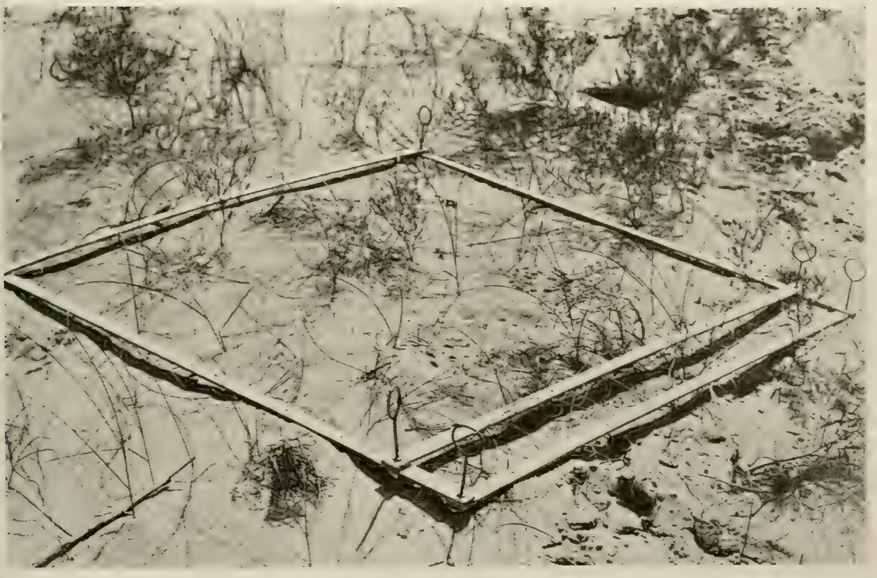


Fig. 2. A later stage in blow-out succession. Besides *Redfieldia* this quadrat shows *Psoralea lanceolata* and *Phaca longifolia*.

PLATE XXXI

Fig. 1. The painted-pod, *Phaca longifolia*, a common blow-out pioneer.

Fig. 2. The blow-out Pentstemon, *P. haydeni*, a common plant of blow-outs.

PLATE XXXII

Fig. 1. The dune-forming habit of *Muhlenbergia pungens.*

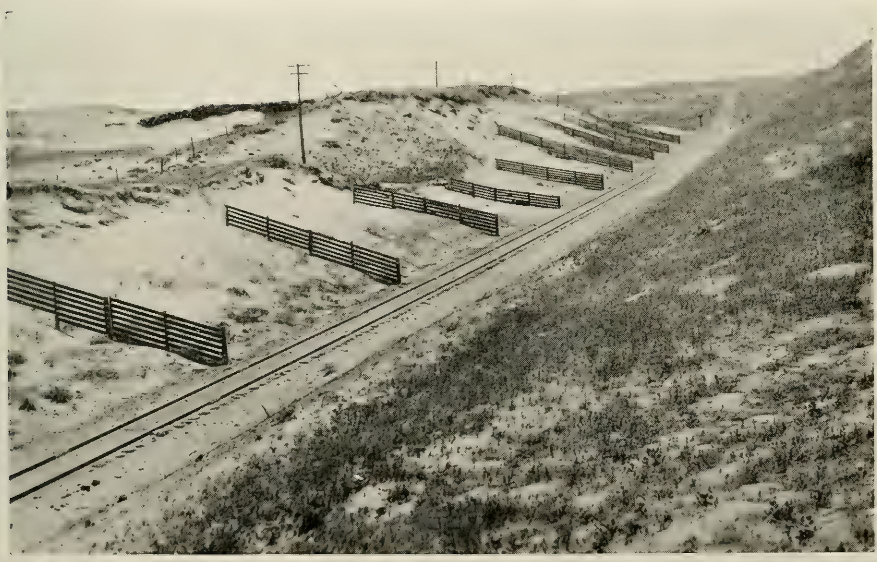


Fig. 2. One type of sand fence adopted by the railroads which pass through the sandhill region.

PLATE XXXIII

Fig. 1. An instrument station on the edge of a large active blow-out.

Fig. 2. *Yucca glauca* and *Muhlenbergia pungens* in an over-grazed area.

PLATE XXXIV

Fig. 1. Sandhills with a fairly uniform cover of spear-grass, *Stipa comata*. There is considerable surface litter and humus here although the sandy nature of the soil is shown along the road.

Fig. 2. The sagebrush, *Artemisia filifolia*, is common in a mixture of types toward the western limits of the sandhill region.

PLATE XXXV

Fig. 1. The woodland formation along the Middle Loup River in Thomas County. The trees here are mostly green ash, *Fraxinus lanceolata.*

Fig. 2. Belts of vegetation along the Middle Loup. In the foreground a belt of short-grass with buckbrush; then a belt of green ash with some *Prunus melanocarpa;* then *Salix humilis,* and bunch-grasses on the hilltop.

PLATE XXXVI

Fig. 1. A hackberry "pocket." The trees are *Celtis occidentalis.* The depression in the center of the clump of trees is due to the presence of the nests of the great blue heron.

Fig. 2. A buckbrush "pocket." The species here is *Symphoricarpos occidentalis.* Note the clumps of *Ceanothus* on the upper slopes and tops of the hills.

PLATE XXXVII

Fig. 1. The woodlands along the Niobrara River in Cherry County. Note the broadleaf species near the river and the conifers toward the top of the hill.

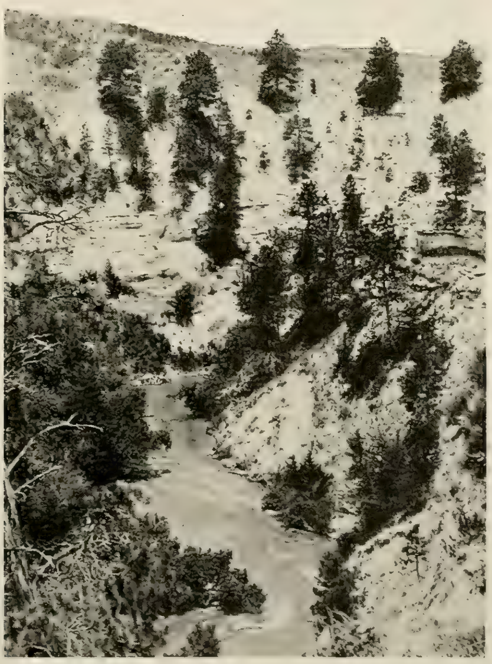


Fig. 2. Snake River Canyon, Cherry County.

PLATE XXXVIII

Fig. 1. Red Cedars, *Juniperus virginiana,* following up a "break" along the Dismal River in Thomas County.

Fig. 2. The water lily association. The marsh formation is dimly seen in the background. Sandhills in the distance.

PLATE XXXIX

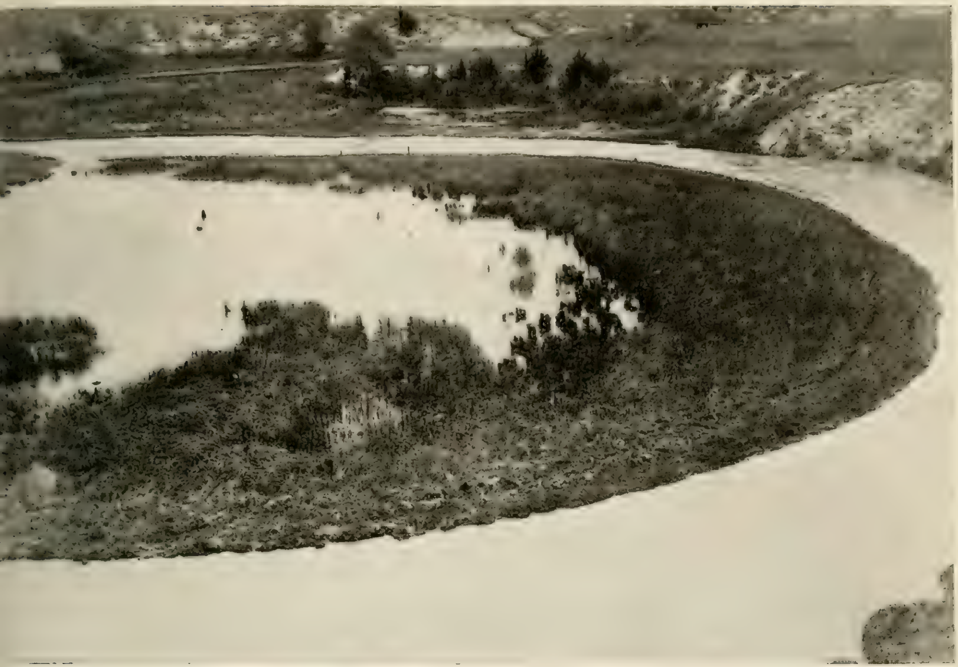


Fig. 1. The streamside marsh in a meander along the Dismal River.

Fig 2. Belt of *Agrostis hyemalis* in a wet meadow. The darker vegetation is mostly *Scirpus, Juncus,* etc. Note the hills with blow-outs and *Yucca* in the distance.

PLATE XL

2. SOME PECULIAR CASES OF PLANT DISTRIBUTION IN THE SELKIRK MOUNTAINS, BRITISH COLUMBIA

Frederic K. Butters

All botanists who have travelled across the Canadian Rocky mountains and the Selkirk range have noted the great differences in the vegetation of the two regions. Indeed these differences are so manifest that they appeal strongly to the average intelligent tourist who crosses these ranges along the main line of the Canadian Pacific railway, stopping perhaps at Banff and Laggan or Field in the Rockies and at Glacier in the Selkirks.

The first difference that appeals to one is the much greater luxuriance of the Selkirk vegetation. This is of course easily explained by the greater rainfall and humidity of the Selkirk range, and, in fact, there are some parts of the eastern Selkirks where the vegetation is but little more luxuriant than in the wetter valleys of the western Rockies. There is, however, a qualitative difference also in the vegetation of the two ranges. The commonest and most characteristic plants about Glacier, for example, are not the same as the characteristic plants of similar altitudes in the Rockies. In general the flora of the Selkirk range is remarkably similar to the flora of regions of like elevation near the Pacific coast, e. g., the subalpine and alpine parts of Vancouver Island, while the flora of the main range of the Rockies is equally similar to that found farther south in Montana, and even in Wyoming and Colorado. The obvious explanation is, of course, the historical one, that the Selkirk plants have migrated in from the west, and the Rocky mountain plants from the southeast, though there is at present little continuity between the Selkirk vegetation and the similar vegetation of the coastal region.

The transition between the Rocky mountain and the Selkirk regions is abrupt. The Columbia valley, lying between the two

ranges, is low (700-750 m.), but narrow. The bottom-lands and bench-lands of the valley seldom occupy more than 10 km. and often the foothills on the two sides of the river approach each other much more closely than this. Even these foothills have, to a large extent, the characteristic vegetation of the range to which they belong.

During the past twelve years the author has spent much time in botanical exploration of the region in question, and has become familiar not only with the country close to the main line of the Canadian Pacific Railway, but also with considerable regions both north and south of that line. It has gradually seemed evident to him, for reasons which will appear later, that the differences in vegetation of the two ranges can be attributed only partially to the combined effects of historical causes and the differences in climate.

It seems well, first, to set forth the peculiar features of the vegetation of three special areas within the Selkirk range, viz.: The moraines of the Sir Sandford glacier, in the northern Selkirks; the limestone ledges of the Cougar valley, near Glacier; and the limestone ledges at the head of Downie creek about 50 km. northwest of Glacier.

1. The Vegetation of the Moraines of the Sir Sandford Glacier

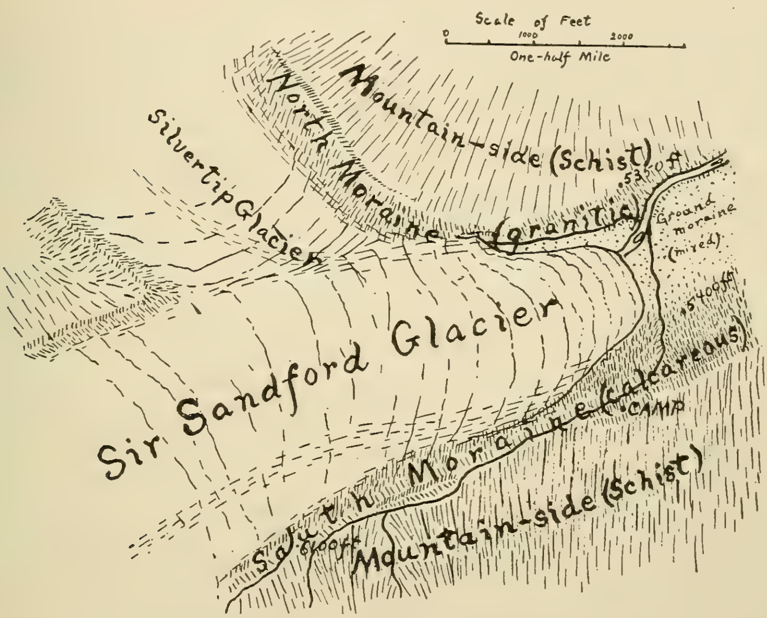
The Sir Sandford glacier is located in the Selkirk range, about 40 km. north of the main line of the Canadian Pacific railway. With its tributaries it drains extensive snowfields lying along the easterly flanks of the Selkirk divide.[1]

During the summers of 1910 and 1911 the author was in camp for about nine weeks on the south moraine of this glacier. Frequent excursions were made throughout the alpine region about Mt. Sir Sandford, and extensive collections were brought back to the Herbarium of the University of Minnesota, where they have since been determined. During these summers the moraines on the north side of the glacier were frequently visited. It soon became evident that the two moraines differ remarkably in vegetation, and with the object of setting forth these differences, thorough collections were made, and numerous field notes were taken relating to various

[1] For accounts of the geography of this region, see papers by Howard Palmer, Explorations about Mount Sir Sandford, British Columbia: The Geographical Journal 27: 170, Feb. 1911, and Observations on the Sir Sandford Glacier, 1911: The Geographical Journal 29:446, May 1912.

questions of the distribution and relative frequency of various species.

The two series of moraines in question are the right and left lateral moraines of the Sir Sandford glacier and the left lateral moraine of the tributary Silvertip glacier which merges with the left Sandford moraine. The region studied is that shown in the accompanying map, and lies between the altitudes of about 5,300 feet (1,600 m.) and 6,500 feet (2,000 m.). No attempt was made to include the moraines lying west of the Silvertip glacier, as they are still actively moving, and bear scarcely any vegetation. The moraines



Map of Tongue of Sir Sandford Glacier, showing position of Moraines. After maps by Howard Palmer.

throughout this region are typical recent moraines, and it seems probable that little if any of the region studied has had its present form for more than three hundred years. This appears to be the approximate age of the most stable portions next to the bounding mountain sides. Extensive portions of the moraines have been stable for 30 to 100 years, while the inner parts are progressively younger, down to the "new" moraine which still rests on the edge of the ice, and is of course constantly shifting and unstable.

As in the case of all recent moraines the soil consists of boulders of all sizes up to occasional ones 10 m. in length. Intimately mingled with these boulders is a large quantity of finer material—small pebbles, sand, and very fine silt or "rock flour." The accumulation of organic matter is very slight owing to the recent origin of even the oldest parts of the moraines, and the small amount of such material formed annually in a region of very short and cool summers. In the newer parts of the moraine (all regions less than 100 years old) the accumulation of humus is entirely negligible. For similar reasons there has been but little weathering of even the finer particles of the soil.

Both moraines are watered by small streams which flow down from the mountain sides and across the moraines, generally flowing for a way obliquely or even longitudinally between parallel ridges of the moraines. These streams have a constant flow, at least during the warm season, being fed by melting snows upon the slopes above. In point of moisture, therefore, the soil varies from the constantly irrigated and sometimes even swampy margins of the streams, to the tops of the ridges which are as dry as any soil can be in a region where the snow lies until June, and a rainless week in summer is less common than a week with seven rainy days.

In all the above respects the north and south moraines are essentially similar. In exposure they differ slightly, the general slope of the south moraine being toward the northwest, the general slope of the north moraine being toward the south. This difference in exposure is really of little importance. There are numerous small ridges with slopes in both directions, and the north moraine, which as a whole gets the most direct sunshine at noon, is shaded by the adjacent mountains during the early morning and late afternoon hours.

In chemical composition, however, the two moraines are entirely different. The south moraine consists largely of fragments brought down from Mt. Sir Sandford, and these are largely crystalline limestone and dolomite. Mingled with these are fragments of mica schist, and a little of a peculiar brown talcose schist which occurs rather widely distributed throughout the Selkirks. The north moraine consists of two portions. The upper, along the side of the Silvertip glacier, is composed of granitic rocks from the mountains at the head of that glacier, mingled with mica schist from the nearer mountains. The lower part has received

contributions also from the mountains to the west and south of the Silvertip glacier, and from the Palisade ridge lying northwest of the upper part of the Sir Sandford glacier. These are largely mica schist, but mingled with it are a few fragments of limestone, and rather more of the brown talcose schist than occurs in the south moraine.

In the following tables the plants of each moraine have been arranged in four lists according to their abundance. In each case table A contains the names of the most abundant plants arranged as nearly as possible in the order of their frequency. The trees have been kept separate from the smaller plants on account of the difficulty of comparing them directly. In the case of the south moraine a special table (I: A, 2) is given, containing the names of the most abundant plants upon the newest moraines, the pioneers of the flora. No similar list was prepared in the case of the left moraine, but the position of several of these plants is indicated by notes in table II: A. Table B is an alphabetical list of all the other plants considered to be abundant. Table C is an alphabetical list of those plants which, although somewhat infrequent, nevertheless occur rather widely distributed. Table D contains the names of plants which are very rare, having been found in only one or two special localities. After each plant name is placed a letter showing where it occurs in the corresponding tables for the other moraine. At the end of these tables, a summary is given showing the relative frequency of species on the two moraines. Four or five doubtful cases due to failure to collect a species in such form that it could be determined have here been included for the sake of completeness. Where there is a possible corresponding species in the other lists, such correspondence has been assumed to exist.

I. TABLES SHOWING THE ABUNDANCE OF DIFFERENT SPECIES UPON THE SOUTH (CALCAREOUS) MORAINE

Table I: A, 1. The most abundant plants arranged approximately in the order of their abundance.

	Occurrence on north moraine	Notes
Trees:		
Picea Engelmanni Parry in Engelm.	C	
Abies lasiocarpa (Hook.) Nutt.	A	
Herbs and shrubs:		
Anemone Drummondii S. Wats.	—	

	Occurrence on north moraine	Notes
Salix artica Pall.	—	
Salix vestita Pursh.	—	
Salix nivalis Hook.	—	
Dryas Drummondii Richards.	—	
Epilobium latifolium L.	A	
Saxifraga aizoides L.	—	
Equisetum variegatum Schleich.	—	Most abundant plant on moist sand flats
Erigeron acris L. var. debilis Gray.	A	
Erigeron uniflorus L.	A	
Dryas octopetala L.	—	
Poa alpina L.	D	
Trisetum spicatum L.	A	Comparatively glabrous form with narrow panicle
Equisetum arvense L.	—	
Cystopteris fragilis (L.) Bernh.	B	
Salix Barclayi Anders.	—	
Salix sitchensis Sanson in Bong.	C ?	

Table I: A, 2. Table supplementary to I: A, 1, showing the most abundant plants on the newer portions of the south moraine in approximate order of frequency.

	Occurrence on north moraine	Notes
Epilobium latifolium L.	A	
Saxifraga aizoides L.	—	
Salix artica Pall.	—	
Salix nivalis Hook.	—	
Poa alpina L.	D	
Dryas Drummondii Richards.	—	
Erigeron acris L. var. debilis Gray	A	
Trisetum spicatum L.	A	
Saxifraga oppositifolia L.	A	
Crepis nana Richards.	—	
Aster Richardsonii Spreng.	—	
Silene acaulis L.	—	

Table I: B. Alphabetical list of plants widely distributed and abundant but less frequent than those of table I: A, 1.

	Occurrence on north moraine	Notes
Anemone multifida Poir.	—	
Antennaria pulvinata Greene.	A	
Arctostaphylos uva-ursi (L.) Spreng.	—	
Arnica Chamissonis Less.	B	
Arnica latifolia Bong.	B	

	Occurrence on north moraine	Notes
Aster Richardsonii Spreng.	—	
Carex nardina Fries.	—	
Castilleja pallida (L.) H.B.K.	—	
Castilleja rhexifolia Rydb.	C ?	
Crepis nana Richards.	—	
Draba lonchocarpa Rydb.	—	
Draba nivalis Liljb.	—	
Epilobium Hornemanni Reichenb.	—	
Erigeron aureus Greene.	C	
Mitella Breweri Gray.	C	
Moneses uniflora (L.) Gray.	—	
Parnassia fimbriata König.	—	
Pedicularis bracteosa Benth.	D	
Populus trichocarpa Torr. and Gray.	—	Small shrubs, apparently never fruiting
Pulsatilla occidentalis (S. Wats.) Freyr.	C	
Salix sp.	—	Probably a hybrid of S. vestita and S. nivalis
Senecio triangularis Hook.	B	In moist shady places
Silene acaulis L.	—	
Solidago multiradiata Ait. var. scopulorum Gray.	D	
Veronica alpina L.	A	

Table I: C. Plants which are infrequent, but which are nevertheless more or less widespread in their occurrence.

	Occurrence on north moraine	Notes
Agoseris sp.	—	
Agropyron biflorum (Brignoli) R. and S.	—	
Arenaria verna L. var. propinqua (Richards.) Fernald.	A	On the north moraine in the smooth form
Artemisia borealis Pallas.	—	
Asplenium viride Huds.	—	
Botrychium lunaria (L.) Sw.	—	
Deschampsia atropurpurea (Wahl.) Scheele.	—	
Epilobium angustifolium L.	C	
Epilobium sp.	—	White flowers
Festuca ovina L.	C	
Fragaria sp.	A ?	
Juniperus communis L. var. montana Ait.	D	

	Occurrence on north moraine	Notes
Leptarrhina amplexifolia (Stern.) Ser.	A	
Parnassia Kotzbuei C. and S.	A	
Pinus albicaulis Engelm.	D	Small shrubs
Polygonum viviparum L.	—	
Ranunculus Eschscholtzii Schlect.	C	
Saxifraga adscendens L.	—	
Saxifraga oppositifolia L.	A	
Senecio pauciflorus Pursh.	—	

Table I: D. Plants occurring only in one or two localities and often under peculiar conditions.

	Occurrence on north moraine	Notes
Achillea millefolium L. var. lanulosa (Nutt.) Piper.	—	No specimen collected, possibly A. borealis
Adiantum pedatum L. var. aleuticum Rupr.	—	One clump under a boulder of talcose schist
Aquilegia formosa Fisch.	—	
Cassiope mertensiana (Bong.) G. Don.	A	A few plants close to the bottom of the inner slope of the old moraine
Cassiope tetragona (L.) D. Don.		
Cystopteris montana (L.) Bernh.	—	On a brown boulder
Oxyria digyna (L.) Hill.	A	Two plants under a brown (talcose?) boulder
Polystichum lonchitis (L.) Roth.	C	
Pyrola sp.	—	Not in flower
Sibbaldia procumbens L.	A	
Taraxacum eriophorum Rydb.	—	
Valeriana sitchensis Bong.	—	

II. TABLES SHOWING THE ABUNDANCE OF SPECIES ON THE NORTH (GRANITIC) MORAINES

Table II: A. The most abundant plants arranged approximately in the order of their abundance.

	Occurrence on south moraine	Notes
Trees		
Abies lasiocarpa (Hook.) Nutt.	A	
Herbs and shrubs		
Oxyria digyna (L.) Hill	D	
Sibbaldia procumbens L.	D	
Gaultheria humifusa (Graham) Rydb.	—	

	Occurrence on south moraine	Notes
Agrostis canina L.	—	
Lutkea pectinata (Pursh) Kuntze	—	Most abundant plant on upper moraine
Epilobium latifolium L.	A	Very abundant on lower, less common on upper moraine
Phyllodoce empetriformis (Smith) D. Don.	—	Most abundant plant on oldest parts of upper moraine
Arenaria verna L. var. propinqua (Richards.) Fernald. forma epilis Fernald.	C	On the south moraine, in the pubescent form
Sagina saginoides (L.) Britton	—	
Saxifraga oppositifolia L.	C	
Erigeron acris L. var. debilis Gray.	A	Larger than on south moraine
Erigeron uniflorus L.	A	
Fragaria platypetala Rydb.	C	
Parnassia Kotzbuei C. and S.	C	
Leptarrhina amplexifolia (Stern.) Ser.	C	
Veronica alpina L.	B	
Artemisia norvegica Fries. var. pacifica Gray.	—	
Antennaria pulvinata Greene.	B	
Phleum alpinum L.	—	
Juncus Drummondii Meyer	—	One of the most abundant plants on new moraines
Juncus mertensianus Bong.	—	One of the most abundant plants on new moraines
Trisetum spicatum L.	A	Very pubescent form with broad panicles
Cassiope mertensiana (Bong.) G. Don.	D	
Phyllodoce glanduliflora (Hook.) Coville.	—	
Empetrum nigrum L.	—	

Table II: B. Alphabetical list of plants widely distributed and abundant, but less frequent than those of II: A.

	Occurrence on south moraine	Notes
Arnica Chamissonis Less.	B	
Arnica latifolia Bong.	B	
Cystopteris fragilis (L.) Bernh.	A	
Juncus Parryi Engelm.	—	

	Occurrence on south moraine	Notes
Luzula Piperi (Coville)	—	
Luzula spicata (L.) D.C.	—	
Lycopodum stichense Rupr.	—	
Saxifraga nootkana Moc.	—	
Senecio trangularis Hook.	B	

Table II: C. Plants which are infrequent, but which are nevertheless more or less widely distributed in their occurrence.

	Occurrence on south moraine	Notes
Aspidium spinulosum (O. F. Müller) Sw.	—	
Aspidium sp.	—	
Botrychium lanceolatum (Gmel.) Angstroem.	—	Only known location in this region
Carex nigricans Meyer.	—	
Castilleja sp.	?	Not in flower
Draba deflexa Greene var. yellowstonensis (A. Nelson) Gilg.	—	
Epilobium angustifolium L.	C	
Erigeron aureus Greene.	B	
Festuca ovina L.	C	
Hieraceum gracile Hook. var. minimum A. Nelson.	—	
Mitella Breweri Gray.	B	
Phegopteris dropteris (L.) Fee.	—	
Picea Engelmanni Parry in Engelm.	A	
Poa Cusickii Vasey.	—	
Polystichum lonchitis (L.) Roth.	D	
Potentilla uniflora Ledeb.	—	
Pulsatilla occidentalis (S. Wats.) Freyn.	B	
Pyrola secunda L.	—	
Ranunculus Eschscholtzii Schlect.	C	
Salix sp.	A ?	Large red-stemmed bush
Vaccinium membranceum Dougl.	—	Small plants

Table II: D. Plants occurring only in one or two localities and often under peculiar conditions.

	Occurrence on south moraine	Notes
Juniperus communis L. var. montana Ait.	C	
Pedicularis sp.	B ?	
Phyllodoce intermedia (Hook.) Rydb.	—	
Pinus albicaulis Engelm.	C	

	Occurrence on south moraine	Notes
Poa alpina L.	A	Very dwarf
Rubus sp.	—	Small bushes, not in flower or fruit
Sambucus sp.	—	Small bushes, not in flower or fruit
Saxifraga bronchialis L.	—	
Solidago multiradiata Ait. var. scopulorum Gray.	B	
Thuja plicata Don.	—	Seedlings
Tsuga mertensiana (Bong.) Carr.	—	Small shrubs
Viola pallens (Banks.) Brainerd	—	

Summary of Tables I and II

Occurrence on south moraine	Occurrence on north moraine A	B	C	D	Total pres't	Abs't	Total on south moraine
A	5	1	2	1	9	10	19
B	2	3	4	2	11	14	25
C	5	0	3	2	10	10	20
D	3	0	1	0	4	8	12
Total present	15	4	10	5	34	42	76
Absent	11	5	11	7	34		Total on both moraines
Total on north moraine	26	9	21	12	68		110

It will thus be seen, that of the 110 species found altogether under the Sir Sandford moraines, only 34 (30.9 per cent) occur on both moraines, while 76 (69.1 per cent) have been found on only one moraine. Moreover, of the 34 which occur on both moraines, 13 (11.8 per cent) differ greatly in abundance in the two cases. This leaves only 21 species (19.1 per cent) which occur with even approximately similar frequency on the two moraines, i. e., which have the same or consecutive index letters in the two cases.

In a similar way, if we take into account only the 68 plants which are listed as abundant (A or B) on at least one moraine, we find that only 11 of these (16.2 per cent) are abundant on both, 17 (25 per cent) are abundant on one and scarce on the other, while 40 (58.8 per cent) though abundant on one moraine have not been found at all on the other.

This great difference in flora is emphasized by the fact that the plants which are found only on the south moraine are nearly all

plants rare in the Selkirk range, and of very local distribution, while those of the north moraine are nearly all the common plants found everywhere in similar situations throughout the region. The flora of the south moraine ceases abruptly where the moraine comes in contact with the schist talus slopes of the adjacent hillsides. These hillsides bear many of the plants found on the north moraine, and almost none of the plants found exclusively on the much nearer south moraine. They have a much richer vegetation and more abundant flora than either moraine as they have been historically much more stable, and have much older soil with a considerable accumulation of humus.[1]

In seeking for the causes of the peculiar plant distributions noted above, it is easily seen that they can not possibly be due to historical reasons. Plants have had equally good opportunities of reaching both moraines. Plants can easily migrate across the region of ground moraine at the foot of the glacier. Seeds of the characteristic plants of the north moraine, growing, as most of them do,

[1]The abrupt transition of vegetation in passing from moraine to hillside is well shown by the following transect, 1 cm. wide, taken across the oldest part of the south moraine and up the adjacent hillside to a height equal to the top of the moraine.

Moraine	
0 m.—1 m.	2 Salix arctica
	4 Moneses uniflora
1 m.—2 m.	1 Salix vestita
2 m.—3 m.	2 Salix vestita
3 m.—4 m.	1 Salix vestita
	1 Salix arctica
	2 Erigeron uniflorus
	1 Anemone parviflora
	1 Antennaria pulvinata
4 m.—5 m.	7 Salix arctica
	2 Salix vestita
	3 Anemone parviflora
	2 Antennaria pulvinata
	1 Erigeron uniflorus
5 m.—6 m.	7 dm. stony
	1 Anemone parviflora
6 m.—7 m.	3 Salix arctica
	2 Dryas octopetala
	2 Anemone parviflora
7 m.—8 m.	2 Dryas octopetala
	2 Abies lasiocarpa (seedlings)
	1 Salix arctica
	1 Salix vestita
8 m.—9 m.	5 dm. stony
	2 Antennaria pulvinata
9 m.—10 m.	6 dm. stony
	1 Arnica sp.
10 m.—11 m.	1 Polystichum lonchitis
	1 Salix nivalis
	1 Picea Engelmanni (seedling)
	1 Saxifraga oppositifolia
11 m.—12 m.	1 Salix vestita
	11.9 m.—12.3 m. stony
12 m.—13 m.	1 Polygonum viviparum
Base of Moraine	
13 m.—15 m.	Bare space beneath large spruce tree
On large limestone boulder fallen from moraine.	
15 m.—16 m.	1 Salix vestita
16 m.—17 m.	2 Salix vestita
17 m.—18 m.	2 Anemone parviflora
	Lichens and moss
Beginning of hillside	
18 m.—19 m.	5 Pyrola secunda
	2 Rhododendron albiflorum
	1 Arnica sp.
	1 Abies lasiocarpa 25 cm. in diameter
19 m.—20 m.	Fallen log
20 m.—21 m.	2 Rubus pedatus
	2 Pyrola secunda
	1 Valeriana sitchensis
	1 Cassiope mertensiana
21 m.—22 m.	4 Rubus pedatus
	1 Rhododendron albiflorum
	1 Vaccinium membranaceum
	1 Cassiope mertensiana
22 m.—23 m.	11 Rubus pedatus
23 m.—24 m.	5 Rubus pedatus
	1 Mitella Breweri
	2 Vaccinium membranaceum
	4 Lutkea pectinata
24 m.—25 m.	6 Lutkea pectinata
	1 Arnica sp.
	1 Luzula Piperi
	1 Mitella Breweri
25 m.—26 m.	7 dm. schist rock, covered with Lutkea pectinata
	1 Mitella Breweri
	1 Luzula Piperi
26 m.—27 m.	Lutkea pectinata throughout
	1 Cassiope mertensiana
	1 Luzula Piperi
	2 Mitella Breweri

on the hillsides on both sides of the glacier tongue, must have reached the south moraine in far greater numbers than the seeds of the plants which actually occupy it—plants in many cases rare in the Selkirk range.

The difference in vegetation must therefore be sought in actual differences in the ability of the two moraines to support certain plants, and, as pointed out in the introductory paragraphs, the moraines are essentially alike in general physical soil composition, in exposure to sunlight, and in water supply. In all these respects there are much greater differences between different portions of the same moraine than between either moraine as a whole and the other moraine as a whole. We are forced to conclude, therefore, that the effective factor is the different chemical composition of the soil—the presence of large quantities of limestone in the right moraine, and its absence from most parts of the left moraine where granitic débris takes its place. It should be further noted that as a limiting factor this chemical difference appears to act directly on the plants, and not through the medium of plant competition. In the newer parts of the moraines the formation is still open, and there is little or no competition. The plants that have become established are usually far apart and there are abundant opportunities between them for any other plant to become established which can grow in the soil and under the somewhat rigorous climatic conditions of the region. Yet a glance at the supplementary table, I: A, 2, will show that exactly the same conditions obtain in these new portions as elsewhere.

The general distribution of the characteristic plants of the south moraine is very interesting. The most abundant rocks of the Selkirk range are quartzites and quartz-schists. Limestones are very rare and local in their occurrence. In the main range of the Canadian Rocky mountains, however, limestones are very abundant, and are present in almost all moraines and talus slopes. Nearly every plant recorded in tables I: A and I: B is abundant in similar situations throughout the Canadian Rocky mountains, while of those not occurring also on the north moraine, many are known to occur elsewhere in the Selkirk range only in a very few places, and then only on known outcrops of limestone, or on débris which, from its situation in relation to such outcrops, presumably contains fragments of limestone. These statements are based largely on personal observations made during nine summers spent largely in these two

ranges, checked by examination of the collections made during that time, and the Selkirk collections of the late C. H. Shaw. A study of the ranges given in Brown and Schäffer's "Alpine Flora of the Canadian Rocky Mountains" bears out these observations. Several technical groups like grasses and willows are not treated in that work, but of the species there listed which appear above as occurring on the south moraine and not on the north, the range of over one-third is given "throughout the Rockies." This indicates that they are sufficiently rare in the Selkirk range so that there were no specimens at hand when that work was being prepared.

The following table gives a list of those plants which are abundant on the south moraine and either entirely absent from the north moraine or very scarce there, together, in each case, with the other known Selkirk stations of the species (except in a few cases where these are very numerous), and notes as to their occurrence in the Rocky mountains.

TABLE III. PLANTS ABUNDANT ON THE SOUTH (CALCAREOUS) MORAINE, AND VERY SCARCE, OR NOT OCCURRING ON THE NORTH (GRANITIC) MORAINE

Anemone Drummondii S. Wats. "Small peak, 118° 20′ W. Long., 51° 45′ N. Lat.[1];" Beaver valley; Copperstain mt., Prairie Hills; Rockies, common.

Anemone multifida Poir. Cougar valley; Rockies, very abundant.

Arctostaphylus uva-ursi (L.) Spreng. Azemuth mt.; Howser lake; Rockies, common.

Aster Richardsonii Spreng. Bishop's range; Cougar valley; Rockies, common.

Carex nardina Fries. "Small peak;" Rockies, present, but apparently not very abundant.

Castilleja pallida (L.) H.B.K. Battle creek; mountain slopes near Mt. Sir Sandford (talcose schist); Copperstain mt., Prairie Hills; "throughout the Rockies," Brown and Schäffer.

Crepis nana Richards. Fish creek valley; Dawson moraine; Glacier Circle; Rockies, abundant.

Draba lonchocarpa Rydb. Two other collections in the region about Mt. Sir Sandford; Rockies, (?).

Draba nivalis Liljb. Cougar valley; Glacier Circle; Rockies, present according to Brown and Schäffer, no specimens collected or seen.

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[1] This is the location given on a number of specimens collected and distributed by the late Charles H. Shaw; it is probably just south of Mt. Sir Sandford, though the stated longitude is too high. It appears to have a thoroughly calciphilous flora. Soil particles from the roots of some of these specimens have been tested, and show a large proportion of calcium. This location will hereafter be cited as "small peak."

Dryas Drummondii Richards. Mouth of Carnes creek; Glacier; Rockies, very abundant.

Dryas octopetala L. "Small peak;" Rockies, abundant.

Epilobium Hornemannii Reichenb. Cougar valley; Bear creek; Prairie Hills; Rockies (?).

Equisetum arvense L. Beavermouth; Howser lake; "alpine meadow 118° 20′ W. Long., 51° 45′ N. Lat.[1];" Rockies, abundant.

Equisetum variegatum Schleich. Fish creek valley; flats of Gold river[2]; flats of the Columbia, Revelstoke; Rockies, common.

Moneses uniflora (L.) Gray. Howser lake; Rockies, common. According to Brown and Schäffer "in mossy spots throughout the region," i. e., Rockies and Selkirks; it is certainly more common in the former range.

Parnassia fimbriata König. Widespread in the Selkirks but local; Rockies more abundant.

Poa alpina L. Avalanche mt., Glacier; flats of Gold river; Prairie Hills; Rockies, common.

Populus trichocarpa Torr. and Gray. Common throughout Selkirks and Rockies.

Salix arctica Pall. Not recorded elsewhere in the Selkirks; Rockies, abundant.

Salix Barclayi Anders. "Alpine meadow;" Rogers Pass; Cougar valley (?); Rockies (?).

Salix nivalis Hook. Fish creek valley; Cougar valley; "small peak;" Rockies, abundant.

Salix vestita Pursh. Only recorded Selkirk station; Rockies, abundant.

Saxifraga aizoides L. Fish creek valley; Dawson moraine; Downie creek valley; Rockies, abundant.

Silene acaulis L. Hermit range; "small peak;" Mt. MacDonald; Rockies, abundant.

Solidago multiradiata Ait. var. scopulorum Gray. Snowsheds, Glacier; Asulkan pass; Prairie Hills; "small peak;" Rockies, abundant.[3]

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[1] Another location where C. H. Shaw collected extensively; it is apparently close to the "small peak;" it will be noted hereafter as "alpine meadow."

[2] Gold river, and its branch, Palmer creek, drain the Sir Sandford range.

[3] In contrast to the above list, the distribution is here given of a few of the characteristic plants of the north moraine:

Cassiope mertensiana (Bong.) G. Don., Phyllodoce empetriformis (Smith) D. Don., and Ph. glandiflorus (Hook.) Coville. Very abundant throughout the Selkirks, abundant in alpine regions in the Rockies which are not excessively calcareous, occasionally found in calcareous areas, but never abundant nor reaching a large size.

There are extensive beds of shale, sandstone, schist, and quartzite in the Rockies, interbedded with the limestones. There are therefore considerable upland areas fairly free from the latter rock. In the lower altitudes the soil almost always contains a considerable proportion of limestone débris.

Gaultheria humifusa (Graham) Rydb. Avalanche Crest, Glacier; Azimuth mt.; Rockies, Yoho valley, soil not calcareous, the only specimen seen from that range. Brown and Schäffer give, "Common in alpine meadows throughout the Rockies and Selkirks;" it is certainly rather uncommon in the former range, and scarcely common in the latter.

Lutkea pectinata (Pursh) Kuntze. The most characteristic Selkirk plant at high altitudes, occurring everywhere except in limestone areas; Rockies, not recorded.

Oxyria digyna (L.) Hill. The distribution of this plant is peculiar. It is the most abundant plant in parts of the north moraine, a single specimen was found on the south moraine, growing under a peculiar brown boulder. It is widely distributed in both Selkirks and Rockies, but very local, sometimes growing in undoubtedly calcareous soil. It grows very abundantly and luxuriantly in an area close to the limestone ledges of Downie creek. Unfortunately no specimens of the soil were taken. Its distribution suggests that it is dependent on the presence of some soil constituent other than lime.

Sibbaldia procumbens L. Local throughout Rockies and Selkirks.

2. The Flora of the Limestone Ledges of the Cougar Valley

The Cougar valley lies just west of the main Selkirk divide, and just north of the main line of the Canadian Pacific railway, entering the Illecillewaet valley about 6 km. northwest of Glacier. The slopes of Cougar mountain, lying west of the valley, are composed of crystalline limestone, and at about 1,800 m. (6,000 ft.) altitude there are exposed and rather dry[1] ledges of this rock. Table IV is a list of the plants collected or noted upon these ledges during two visits to them. It is probably not exhaustive. Notes of distribution are given for each species as in Table III, except where they have already been given.

TABLE IV. PLANTS OF THE LIMESTONE LEDGES OF THE COUGAR VALLEY

Abies lasiocarpa (Hook.) Nutt. Abundant in both Selkirks and Rockies.

Anemone parviflora Michx. Revelstoke; valley of Palmer creek below the Sir Sandford glacier; upper Beaver valley; Rockies, abundant.

Anemone multifida Poir.

Arabis Lyallii S. Wats. Widespread, but very local in its occurrence in the Selkirks, about one-half the specimens recorded as on limestone; Rockies, common.

Arenaria sajanensis Willd. Donkin Pass (talcose schist); Mt. Cheops; "small peak;" Rockies, not very abundant.

Asplenium viride Huds. South moraine, Sir Sandford glacier; head of Downie creek; "51° 30′ N. Lat.;" Rockies, frequent.

Cassiope mertensiana (Bong.) G. Don. Less abundant here than elsewhere in the region, common in both Selkirks and Rockies.

Cystopteris fragilis (L.) Bernh. Frequent in Selkirks but local, very common in Rockies.

Draba crassifolia Graham. Glacier Circle; slopes west of Silvertip névé, Mt. Sir Sandford region (soil not calcareous); "small peak[2];" Rockies; present, but apparently not abundant.

Draba deflexa Greene. Avalanche Crest, Glacier; slopes west of Silvertip névé, Mt. Sir Sandford region; Rockies, abundant.

Draba deflexa Greene var, yellowstonensis (A. Nelson) Gilg. Glacier Circle; north moraine, Sir Sandford glacier; Rockies, abundant.

Draba nivalis Liljb.

Epilobium angustifolium L. Very abundant throughout the Selkirks and Rockies.

Epilobium Hornemannii Reichb.

Epilobium latifolium L. Abundant throughout both ranges.

Erythronium grandiflorum Pursh. Abundant but local in both ranges.

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[1] Only edaphically dry; the valley has the reputation of being the rainiest in the vicinity of Glacier. The ledges may be actually dry during two or three weeks in the course of a summer.

[2] Shaw collection No. 1051, distributed as D. nivalis.

Mitella Breweri Gray. Widely distributed but somewhat local in the Selkirks; Rockies, abundant.

Mitella pentandra Hook. Distribution similar to M. Breweri.

Mitella trifida Graham var. violacea (Rydb.) Rosendahl. Very rare; the only other specimens of this species from this region are from Carbonate Draw (upper Columbia valley) and Lake Louise (Rockies). The latter is the typical species.

Poa glauca Vahl. Avalanche mt., Glacier; Rockies, no specimens.

Ranunculus Eschscholtzii Schlect. Widely distributed in the Selkirk range, but local; Rockies, very abundant.

Ribes lacustre (Pers.) Poir. Widely distributed in the Selkirks; Rockies, very abundant.

Salix nivalis Hook.

Salix sp., shrub 1 m. tall, possibly S. Barclayi. Unfortunately the specimens have been mislaid.

Saxifraga nivalis L. "Small peak;" Rockies, very abundant.

Sedum stenopetalum Pursh. Bishop's range; Rockies, fairly common.

Selaginella densa Rydb. Avalanche Crest, Glacier; mountain above Revelstoke; "small peak;" Rockies, very abundant at high altitudes.

Thalictrum occidentale Gray. Avalanche Crest, Glacier; "alpine meadow;" "frequent throughout the Rockies" according to Brown and Schäffer.

Vaccinium membranaceum Dougl. A few small plants on these ledges; Selkirks, very abundant throughout; Rockies, rare.

Valeriana sitchensis Bong. Frequent throughout the Selkirks; Rockies, less abundant.

I have a record of a single small hemlock tree, Tsuga heterophylla (Raf.) Sarg., growing on these ledges. The two hemlocks, Ts. heterophylla, and Ts. mertensiana (Bong.) Carr. are very scarce and stunted in the calcareous parts of this valley, in marked contrast to their large size and abundance in neighboring valleys, and throughout the Selkirk range generally. They are not recorded from the Rockies.

3. The Flora of the Limestone Hedges near the Head of the Valley of Downie Creek

A short distance north of the pass between the head of the North Fork of the Illecillewaet river and the head of Downie creek, there are extensive cliffs of a dark gray, massive limestone. This region is about midway in latitude between the two previously discussed and lies farther west than either of the others, although like the Cougar valley it is just west of the Selkirk divide. Several plants, otherwise rare or unknown in the Selkirk range, were found upon these ledges or among the adjacent débris.

TABLE V. CERTAIN PLANTS OF THE LIMESTONE AREA AT THE HEAD OF DOWNIE CREEK

Arabis Lyallii S. Wats.

Asplenium viride Huds.

Cryptogramma Stelleri (Gmel.) Prantl. Only recorded Selkirk station; Rockies, "not common," Brown and Schäffer.

Gentiana amarella L. var. acuta (Michx.) Herder. Only recorded Selkirk station; Rockies, very abundant.

Lappula floribunda (Lehm.) Green. Nelson; Rockies, very abundant.

Potentilla dissecta Pursh. "Small peak;" the var. glaucophylla occurs on Avalanche mt., Glacier, and Copperstain mt., Prairie Hills; Rockies, both forms are apparently common.

Saxifraga punctata L. Asulkan valley; Rockies, local.

Saxifraga mertensiana Bong. Prairie Hills; Avalanche Crest, Glacier; Cougar valley; Rockies (?).

Shepherdia canadensis (L.) Nutt. Howser lake; Gold stream, both at low elevations; the only station recorded well within the Selkirk range; very abundant in the Rockies, and in the low valleys bounding the Selkirk range.

Conclusion

In the foregoing pages it has been shown that a considerable number of plants which form characteristic parts of the Rocky Mountain vegetation occur in the Selkirk range, some of them at many widely separated points. These plants obviously have not been historically unable to reach the Selkirks. Some of them, like those occurring near the head of Downie creek, have penetrated more than half-way across the range. The areas where they occur have the typical Selkirk climate, and there is nothing about this which interferes with their growth. Where they are found they are usually flourishing and bear an abundance of seeds. Apparently the only explanation of their extremely local occurrence in the Selkirks is the explanation put forth in section 1 of this paper, that they require soils containing limestone, and that they grow with great difficulty, or not at all, in its absence. The great abundance of limestones in the Canadian Rocky mountains renders practically all the mixed soils of that range calcareous, and so allows these plants to occur abundantly throughout the region. On the other hand the characteristic Selkirk rocks are quartzites and schists rich in quartz and very poor in lime.[1] Many of the plants which

[1] Granite is exceptional, occurring in those parts of the range which are personally known to the author, only in the region northwest of Mt. Sandford, and in Battle creek valley, a little-known region about twenty-five miles south of Glacier.

flourish on the somewhat sour soils formed by these rocks seem to be largely inhibited by the presence of lime, and hence in the Rocky mountains they are uncommon or absent, just as they are absent from the limited limestone areas just discussed.[1] The differences then in the characteristic vegetation of the two ranges seem to be due not only to the historical differences which undoubtedly occur,[2] and to the climatic differences which also have considerable effect, but also, and to a very large extent, to the great differences in the constituent rocks of the two ranges, and in the soils which have been derived from them.

Similar instances have been noted many times in Europe, and recently similar peculiarities in the distribution of the alpine plants of eastern North America have been noted by Fernald.[3] It is interesting to note how regularly the distribution of plants as noted by Fernald for New England and the region about the Gulf of St. Lawrence agrees with the observations which have been made by the author in the mountains of British Columbia, a portion of which have been set forth in the present paper. Of 34 plants mentioned both in the present paper, and by Fernald, 20 appear to have exactly the same type of soil distribution in the two regions, the others appear to be less particular in their soil requirements in one or the other region. In no case is there a reversal of soil requirement as between the two regions, and the same proportion holds good in the case of the numerous other plants mentioned by Fernald and occurring in the Rocky and Selkirk ranges, though not in the districts covered by this paper.

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[1] A number of them occur locally in the Rockies. The soils in which they are found have not been tested, but their distribution suggests that they are found on the scattered quartzite areas of that range, and that they therefore represent the converse of the peculiar distributions discussed above.

[2] An interesting case of this is the total absence from the Selkirk range, so far as is known, of the numerous species of *Astragalus*, *Oxytropis*, and *Hedysarum* which are abundant in the Rockies. These plants would undoubtedly grow well upon the calcareous areas noted above, but with their poor means of migration they have been unable to reach these small and isolated areas.

[3] M. L. Fernald, The Soil Preferences of Certain Alpine and Subalpine Plants: Rhodora, 9:149, 1907.

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CONTENTS

THE DEVELOPMENT OF CLIMAX FORMATIONS IN NORTHERN MINNESOTA

H. F. Bergman and Harvey Stallard

The climax vegetation of a region is the result of all the forces operative upon it during its development, its general features being determined by the climate. Within a region the same final or climax stage results through a series of developmental or successional stages, whether starting from open water, solid rock, or denuded land.

It is the purpose of this paper to trace the successions from the initial to the climax stage in northern Minnesota, as well as the forces that have operated together to produce the climax or earlier stages of stabilization. These processes may be expected to continue without change, unless disturbed by a reversal of climatic conditions or by any other change which would seriously affect the water or light relations of the dominants in the climax.

The results here presented are based upon field work which has extended over a period of four years and has involved the study of coniferous and deciduous forest, swamp, and other developmental stages in different parts of the state. The work has been of an exact nature, with quadrats and instruments, so that definite information has been obtained as to the structure of vegetation of the climax stages and of the successional stages leading up to the climax, as well as of the factors concerned in the development.

The work was undertaken at the suggestion and under the direction of Dr. Frederic E. Clements, to whom the writers are indebted for invaluable suggestions and criticisms, and particularly for his kindness in placing freely at their disposal his work on *Plant Succession,* which has been used in the preparation of this report. The classification of successions and of the causes initiating

them and leading up to the development of the climax formations, as well as the terminology used, are those proposed by Clements in *Plant Succession.* The nomenclature of ferns and flowering plants is essentially that of the seventh edition of Gray's *Manual.*

Climax Formations

Minnesota may be divided into three great regions according to the final or climax vegetation which dominates them, viz., pine forest, deciduous forest, and prairie. The distribution of the three climax formations may be indicated by the accompanying map (figure 1).

Classification of Successions

It has been customary to classify successions according to the initial cause, but it has been pointed out by Clements (1916) that such a classification is unnatural and unsatisfactory, since the same climax type may result from several different initiating causes. Successions are accordingly classified as follows:

I. Primary Succession
  1. Hydrarch
  2. Xerarch

II. Secondary Succession

Whether a succession is to be primary or secondary is determined by the initial cause which, by the extent to which the habitat is disturbed, affects the kind and amount of water present. Primary successions may be subdivided into hydrarch and xerarch successions, depending upon the character of the initial stage. Those beginning in water are called hydrarch, those beginning in dry conditions, xerarch (Cooper 1912).

COURSE OF SUCCESSION

The course of succession is indicated by the zonation peculiar to a region. Accordingly, the key to the order of succession and to the factors which have controlled it is to be found in the study of zonation and the existing conditions of the different zones, or their corresponding associes.

In tracing the development of the climax, the effect of the various causes of succession in producing new habitats will first be considered briefly. In turn, the effect of the ecesic and stabilizing causes in determining the nature of the development to the final

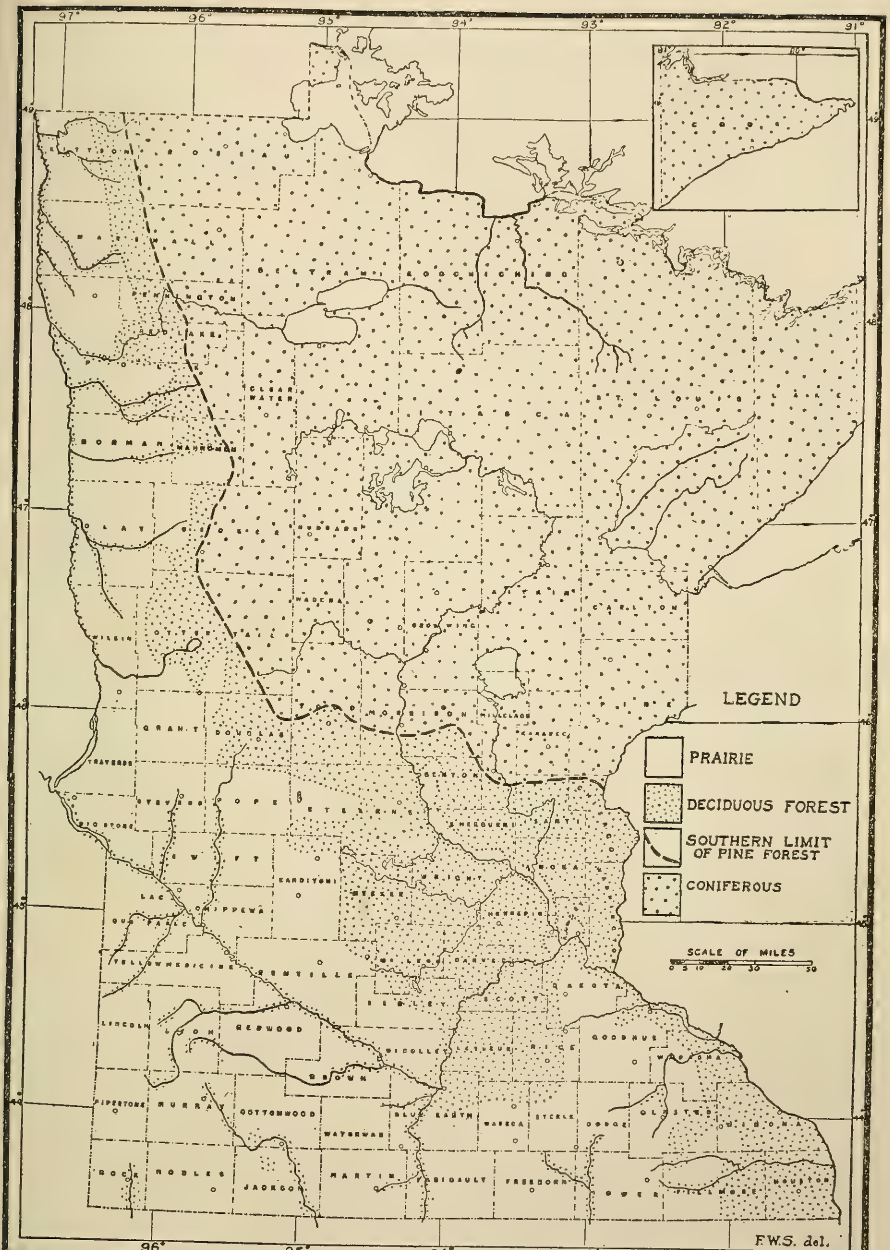

Fig. 1. Map of Minnesota showing distribution of climax formations. (Reproduced from fig. 14, Bulletin No. 12, Minnesota Geological Survey.)

climax for each of the principal successions in each of the climax associations will be discussed.

PINUS STROBUS-PINUS RESINOSA ASSOCIATION

I. Primary Succession

Initial causes: Wherever water collects in sufficient quantities to destroy completely any vegetation which may have existed previously in the area covered, a primary succession may begin. The lakes of Minnesota are largely due to glaciation, by which the drainage systems that had developed during the time from the Cretaceous period down to the glacial epoch were more or less completely blotted out, causing the development of new drainage channels. The deposition of glacial till on the retreat of the ice-sheet also blocked many of the drainage channels, causing the lower areas to become filled with water from the melting ice. Some of the lakes in northeastern Minnesota probably existed essentially in their present form before the glacial period, occupying the troughs of the central folds that have occurred in the earth's surface. Such lakes have rock-bound shores and are usually long, narrow, and deep. Owing to the hardness of the rocks forming their shores, they probably were little affected by the passage of the continental glacier.

The effects of climate as initial causes since the glacial period are of less consequence. The flooding of areas by man or by beavers would initiate a primary succession if the areas were flooded to sufficient depths. There is no evidence, however, that primary successions in Minnesota have been initiated by biotic agencies.

1. HYDRARCH SUCCESSION

This succession, which has its origin in water and culminates in the *Pinus strobus-P. resinosa* climax association, shows a series of stages which may be indicated as follows:

(1) *Chara-Philotria* Associes
(2) *Castalia-Nymphaea* Associes
(3) *Scirpus-Zizania* Associes
(4) *Carex* Associes
(5) *Chamaedaphne-Andromeda* Associes
(6) *Larix-Picea* Associes
(7) *Abies-Betula* Associes
(8) *Pinus* Association

Variations of this sequence may sometimes occur by the omission or slight development of a stage, or within an associes by the disappearance of one or more of its consocies. Such variations will be indicated in the discussions of the associes of the successions and more fully treated in a later report.

(1) *Chara-Philotria* Associes

This associes appears only in deep water, varying in depth from six to twenty feet. In such places succession may begin with the invasion of *Chara, Philotria,* and other dominants of the associes. The character of the bottom plays a part in the ecesis of these plants. On sandy or muddy bottoms they establish themselves readily, but on coarse gravel or rock this is not possible. The lakes of northeastern Minnesota, which occur in basins of rock, are accordingly devoid of submerged aquatics.

Consocies: *Chara* is the first species to invade the lake bottoms, and consequently in the deeper places is often the only species present. In somewhat shallower water, perhaps to a depth of fifteen feet, *Utricularia vulgaris* appears, and associated with it are *Philotria canadensis* and *Myriophyllum* sp. *Utricularia, Philotria,* and *Myriophyllum* extend from the deeper water out to the *Castalia-Potamogeton* zone; they are always submerged, but often form very dense masses of vegetation.

Secondary species: Associated with them in water up to ten or twelve feet in depth are: *Potamogeton perfoliatus* and *Potamogeton zosteraefolius.*

(2) *Castalia-Nymphaea* Associes

The principal natural causes contributing to the development of this associes are: (1) the deposition of material eroded by streams and transported into the lake, filling it up until the species of the associes are able to enter and establish themselves, (2) the accumulation of decayed remains of the pioneer plants of the lake bottoms. The latter cause works very slowly in comparison with the establishment of plants of the following associes. Drainage of the lakes, if not complete, would lower the water-level so that plants of this associes would find favorable conditions for growth.

Consocies: Three species are typically found as consocies in this associes:

Castalia odorata *Potamogeton natans*
Nymphaea advena

While these three species are generally associated, combinations of any two of them may occur, and in some instances only a single species is to be found representing the associes. These species grow in water from one to six feet in depth, the best development being in from two to six feet of water.

The following plants occur more or less abundantly as secondary species of this associes:

Ceratophyllum demersum *Potamogeton pectinatus*
Myriophyllum sp. *Utricularia vulgaris.*
Potamogeton perfoliatus *Zannichellia palustris*

Polygonum amphibium and *Batrachium trichopyllum* occur occasionally in this zone, but never very abundantly. Among the other plants, floating on the surface, are to be found duckweeds in more or less abundance. The growth of waterlilies so that their leaves cover the surface of the water more or less completely greatly checks or prevents the development of submerged aquatics.

(3) *Scirpus-Zizania* Associes

The reaction of the plants of the *Castalia-Nymphaea* associes in retaining and binding into a soil the sedimentary material washed into the lake, as well as by the accumulation of the decayed remains of the water-lilies and pondweeds, causes the lake shore to be built up more rapidly, thereby enabling *Scirpus, Zizania,* and other species of this associes to invade and become established.

The lowering of the water-level by partial drainage of a lake or by any other cause would result in the movement of the *Castalia-Nymphaea* zone out into deeper water to be replaced by the *Scirpus-Zizania* zone, or if the lowering of the water-level were sufficient the latter would invade to the exclusion of the former.

Consocies: The associes consists of several consocies which may occur all together or in various combinations; or, in other instances, a single consocies may be the only representative in this stage of development. The typical consocies are:

Phragmites phragmites *Typha latifolia*
Scirpus occidentalis *Zizania aquatica*
Scirpus validus

Equisetum fluviatile often occurs as a socies in this associes. It seems to thrive best on a silty bottom in a depth of one to three feet of water. In places it forms rather extensive areas of pure growth, notably on Leech Lake near the mouth of Boy River and at the west end of Long Lake near Ely. Usually, however, *Equisetum* occurs mixed with other species of the associes.

The distribution of the consocies depends upon the character of the lake shore. *Scirpus* is able to establish itself in well-packed sand or sandy gravel, and where the lake shore is of this character, *Scirpus* is usually or often the only species present. It may become established on a lake shore and extend out to a depth of six or eight feet of water without being preceded by the *Chara-Philotria* and *Castalia-Nymphaea* associes of the normal succession. Lake shores of pure, packed sand occur where the shore is subject to heavy wave-action or to a limited amount of ice-action. On shores much exposed to wind-driven ice, the force with which the ice masses are carried is sufficient to plow up the shore, completely preventing the establishment of *Scirpus* or other plants and often forming an abrupt wall or bank along the shore exposed.

Zizania is able to establish itself only where the shore or bottom of a lake or river is covered with silt or with a considerable amount of decayed plant remains, and consequently is not found in parts of lakes subject to much wave-action or to the action of wind-driven ice. This is true also of *Phragmites* and *Typha,* but apparently *Phragmites* may become established where *Zizania* can not, either because of the bottom or because of too much wave-action.

Phragmites may be the first invader in a lake, but usually not beyond a depth of two or three feet. Examples of this are to be found along the south and west shores of Ball Club Lake and on the west side of Little Winnebegoshish, and the Mississippi River for a short distance above where it flows into Little Winnebegoshish. It also occurs in abundance in Lake of the Woods from the mouth of Rainy River to Oak Point, where it grows in five feet of water, the maximum depth observed.

Secondary species: Various duckweeds are to be found floating on the surface, and as submerged plants different kinds of algae, as well as *Potamogeton, Myriophyllum, Utricularia, Batrachium,* etc., occur. The characteristic secondary species of this associes are the following:

Acorus calamus	*Polygonum amphibium*
Alisma plantago	*Sagittaria arifolia*
Eleocharis palustris	*Sparganium eurycarpum*
Naumbergia thyrsiflora	

The last two named are never abundant, but are usually represented by a few individuals. *Naumbergia* becomes more abundant in the following associes.

(4) *Carex* Associes

The reaction of the plants of the *Scirpus-Zizania* associes in building up the lake shores, by retaining the sedimentary material washed into the lake and by the accumulation of decayed plant remains, results in a lowering of the water-level. This permits the invasion and establishment of species of *Carex*, which are the dominants of this associes. The lowering of the water-level of the lake by drainage or by any other cause would bring about a change of conditions favorable for the establishment of species of this associes.

Consocies: Several species of *Carex* are the dominants of this state. The following are the typical species:

Carex aquatilis	*Carex trichocarpa*
Carex filiformis	

Carex aquatilis and *C. filiformis* are less abundant than *C. trichocarpa*, although in some places *C. filiformis* occurs exclusively. Usually the *Carex* zone is narrow, varying from three or four feet to thirty or forty, although in exceptional cases it may be much wider. In many instances the *Scirpus-Zizania* associes is poorly developed, being represented by a sparse growth of *Zizania* or of *Zizania* and *Scirpus*, or it may be entirely absent, the *Carex* associes directly following the *Castalia-Nymphaea* associes. The sedges push out farther into the water from year to year by the development of rootstocks and cause a rapid filling of the lake, thus enabling the following associes to become established.

Secondary species: The following species of sedges and grasses are usually present, but with the exception of *Carex diandra* never appear in sufficient number to be regarded as consocies. This may be true of *Carex diandra* in some cases.

Carex bebbii	*Carex sartwelli*
Carex diandra	*Phalaris arundinacea*

The following species of herbs are characteristic:

Alsine longifolia	*Galium trifidum*
Aster paniculatus	*Mentha canadensis*
Campanula aparinoides	*Naumbergia thrysiflora*
Cicuta bulbifera	*Rumex verticillatus*
Dryopteris thelypteris	*Scutellaria galericulata*

Galium, Campanula and *Alsine* form a ground layer under the sedges and grasses, and often make very dense growths, particularly the first two.

The following species often occur with this associes, but are usually not present in great number:

Asclepias incarnata	*Eupatorium purpureum*
Caltha palustris	*Iris versicolor*
Carduus muticus	*Lathyrus palustris*
Comarum palustre	*Menyanthes trifoliata*
Epilobium lineare	*Persicaria amphibia*
Equisetum fluviatile	*Rumex occidentalis*
Eriophorum polystachyon	

(5) *Chamaedaphne-Andromeda* Associes

The appearance of *Sphagnum* in pools of water between the tufts of *Carex* is made possible by the advancing *Carex* which builds a substratum at or above the water-level of the lake or pond. *Sphagnum* then colonizes about the clumps of *Carex* or in pools of shallow water between tufts. Although in Europe *Sphagnum* has often been observed to invade open water this has not been found to occur in Minnesota. The replacement of the *Carex* stage by the bog heaths is usually attributed to an increase in the acidity of the water owing to the presence of *Sphagnum,* but from repeated observations in numerous swamps it seems that there is not a sufficient increase in acidity to account for this. It is not possible at this time to state the cause of the replacement of *Carex* by *Sphagnum* and species of bog heaths, but in some way the reaction of the *Carex* stage is unfavorable to its continuance while it is distinctly favorable to the development of *Sphagnum.* The appearance of *Sphagnum* provides conditions suitable for the invasion of *Andromeda, Ledum* and others of this associes.

Consocies: The following plants are the typical consocies:

Chamaedaphne calyculata, Andromeda glaucophylla and *Ledum groenlandicum. Andromeda* and *Chamaedaphne* make their appearance very soon after *Sphagnum,* so that before the latter has completely occupied the area, the bog heaths have appeared. By the time that *Sphagnum* has formed a complete zone, the bog heaths have developed a complete zone also.

In the fully developed associes, *Ledum groenlandicum* usually appears as one of the consocies, but in some instances it does not occur at all. When *Ledum* does appear, it is at a later stage than the other two. *Kalmia glauca* is sometimes present, but hardly in sufficient quantity to be called a consocies. It is abundant northward, and occurs rarely in other places. Either *Chamaedaphne* or *Andromeda* may be the first successor of the pioneer *Sphagnum,* or both may appear at essentially the same time.

A few cases have been observed where *Salix candida, S. myrtilloides,* and *S. petiolaris* and *Betula pumila* were the first invaders of the *Carex* associes, to be followed by the development of *Sphagnum* and soon afterward by *Ledum.* It seems rather probable, however, that this is a disturbance of the normal primary sequence due to the partial secondary succession initiated by lumbering or flooding.

Secondary species: Along with *Andromeda* and *Chamaedaphne,* on the hummocks of *Sphagnum,* is usually to be found a more or less extensive development of *Oxycoccus macrocarpus* and *O. oxycoccus.* The *Chamaedaphne-Andromeda* associes is further marked by the presence of very characteristic herbs, among which *Sarracenia purpurea, Drosera rotundifolia,* and *Smilacina trifolia* are most typical. *Saxifraga pennsylvanica, Eriophorum angustifolium* and *E. gracile* are sometimes found. *Menyanthes, Comarum* and others of the preceding *Carex* associes occur also.

(6) *Larix-Picea* Associes

The formation of *Sphagnum* mounds builds up the substratum above the water-level and provides far better aeration, and thus furnishes suitable conditions for the invasion of *Larix* and *Picea,* which become established, and finally form such a dense growth that the *Chamaedaphne-Andromeda* associes disappear completely.

Consocies: There are two trees that are the typical consocies in this associes, viz., *Larix laricina* and *Picea mariana.*

Larix is the first invader of the *Chamaedaphne-Andromeda* scrub, and in some cases may be the sole representative, except for

a more or less indefinite zone of *Picea* along the border of the swamp. *Larix* ranges farther to the south than *Picea,* so that the latter is less abundant as the southern limit of its range is approached. Usually *Larix* and *Picea* are intermingled, or sometimes *Picea* becomes more abundant and replaces *Larix* more or less completely.

When *Larix* is the most abundant species, the growth is less dense, and the smaller reduction of the light intensity may enable the shrubs of the *Chamaedaphne-Andromeda* associes to persist as long as *Larix* remains the dominant. *Andromeda* and *Chamaedaphne* disappear first, as they are unable to endure shading, but *Ledum* may persist as long as the swamp itself remains.

When the bog becomes filled up with partly decayed *Sphagnum* and rotted wood, or filled around the edges by the washing in of soil from the sides, *Picea* and *Thuja* may replace *Larix* completely. When they become more numerous than the tamaracks, the shrubs of the *Chamaedaphne-Andromeda* associes disappear, and the succession advances to the next stage.

If very extensive areas are occupied by this associes, it may persist indefinitely as a subclimax, owing to the slowness with which changes take place that would make possible the invasion and establishment of species of the following *Abies-Betula* associes. The natural development may be retarded by burning or lumbering, or may be accelerated by draining.

Secondary species: In addition to *Andromeda, Chamaedaphne,* and *Ledum,* which belong typically to the preceding stage but persist in the *Larix-Picea* associes, the following occur as characteristic shrubs of this associes: *Ribes hudsonianum, R. triste, Rhamnus alnifolia* and *Lonicera oblongifolia.* Many of the herbs which occur in the *Chamaedaphne-Andromeda* associes are still to be found in this stage. Others are characteristic of this associes, since in a regular sequence of stages they appear here for the first time and find their best development here. The following herbs occur on hummocks of living *Sphagnum:*

Drosera rotundifolia	*Sarracenia purpurea*
Eriophorum gracile	*Saxifraga pennsylvanica*
Mitella nuda	*Smilacina trifolia*
Oxycoccus oxycoccus	*Viola blanda*

With the exception of *Mitella* and *Viola,* the plants of the above

list are relicts of the preceding associes. With these species may also be found:

Carex gynocrates	*Carex trisperma*
Carex leptalea	*Coptis trifolia*
Carex paupercula pallens	*Habenaria dilatata*
Carex scirpoides	*Habenaria hyperborea*
Carex tenella	*Habenaria obtusata*

Where *Sphagnum* has died out leaving mounds of humus, and along the border of the swamp where filling up has resulted in death of the *Sphagnum*, the following plants are characteristic:

Carex tenella	*Linnaea borealis*
Carex trisperma	*Maianthemum canadense*
Chiogenes hispidula	*Osmunda cinnamomeum*
Clintonia borealis	*Osmunda claytoniana*
Coptis trifolia	*Petasites palmata*
Cornus canadensis	*Pyrola asarifolia*
Cypripedium hirsutum	*Pyrola secunda*
Cypripedium parviflorum	*Trientalis americana*
Dryopteris cristata	

Chiogenes and *Linnaea* are found often on decayed fallen logs, where they usually form a dense mat over the surface. Many of the plants of the above list are to be found typically on swamp borders. *Gaultheria procumbens* has been found occasionally with the above plants.

(7) *Abies-Betula* Associes

The filling-up of a swamp by the washing in of soil from the sides and in part also by the accumulation and subsequent decay of *Sphagnum* and other plant remains results in the formation of a soil rich in humus, but one in which the water-content is much reduced as compared with that of the substratum of the *Larix-Picea* or *Chamaedaphne-Andromeda* associes. The formation of humus and reduction of water-content favors the invasion and establishment of the plants of the *Abies-Betula* associes. Drainage of a swamp would accelerate the appearance of subsequent stages.

Consocies: The following are the usual dominants: *Abies balsamea, Betula papyrifera, B. lutea, Picea canadensis* and *Thuja occidentalis.*

All of these are not found together in any given area or zone, but in the stage of development from spruce-tamarack swamps to the finally dominant pines, combinations of any two or more of these may occur. By aggregation, families or colonies of any one of the above may occur and are frequently encountered. Pure dominance of any of them is rare.

Secondary species: Characteristic undershrubs of this associes are:

Acer spicatum	*Rhamnus alnifolia*
Alnus incana	*Rhus rydbergii*
Cornus stolonifera	*Ribes americanum*
Corylus rostrata	*Ribes hudsonianum*
Lonicera hirsuta	*Ribes prostratum*
Lonicera oblongifolia	*Rosa acicularis*
Parthenocissus quinquefolia	*Viburnum lentago*
Prunus pennsylvanica	*Viburnum pubescens*
Prunus virginiana	

Semi-woody plants such as *Diervilla lonicera* and *Rubus triflorus* are usually present.

Amelanchier oblongifolia and *Sorbus americana* occur occasionally. *Lonicera oblongifolia* and the last two species of *Ribes* persist from the preceding associes, or from it may invade the adjacent *Abies-Betula* associes. In some places *Rosa blanda* replaces *R. acicularis*.

The following herbs are commonly found:

Aralia nudicaulis	*Equisetum sylvaticum*
Carex tenella	*Galium triflorum*
Carex trisperma	*Maianthemum canadense*
Clintonia borealis	*Mitella nuda*
Cornus canadensis	*Rubus triflorus*
Dryopteris cristata	*Streptopus roseus*
Dryopteris phegopteris	*Trientalis americana*

Occasional plants of *Actaea rubra* may be found with the above.

(8) *Pinus* Association

The further filling of a swamp by the carrying in of soil from the sides and by the accumulation of decayed plant-remains brings about a reduction of the water-content of the soil. The habitat has

now become completely mesophytic in character. The reduction of water-content and the ability of pine seedlings to grow in a reduced light makes it possible for pines to invade and to become established. The actual invasion of the *Abies-Betula* zone must occur in the spaces between more widely separated individuals of that zone. The destruction of members of the *Abies-Betula* associes by diseases, insects, the breaking and uprooting of trees by wind, all contribute to the formation of openings in which pines may invade and establish themselves. The greater longevity of pines as compared with *Abies, Betula* and *Picea* enables the pines to become dominant in competition with them.

Consocies: The dominant species of pines of the climax forest are *P. strobus* and *P. resinosa.* The two species often occur in a mixture, or extensive tracts may be occupied by either as a pure dominant. It seems probable that *P. strobus* would finally replace *P. resinosa,* but at present this cannot be confirmed.

Secondary species: Shrubs are usually absent in the well-developed climax. The following low shrubs and herbs are the characteristic plants of the usually sparse ground layer:

Anemone quinquefolia	*Maianthemum canadense*
Chimaphila umbellata	*Pyrola americana*
Cornus canadensis	*Pyrola secunda*
Diervilla lonicera	*Vaccinium canadense*
Gaultheria procumbens	*Vaccinium pennsylvanicum*
Lycopodium obscurum	

Antennaria canadensis, Lycopodium annotinum and *Pyrola elliptica* occur occasionally. *Epigaea repens* is found in certain areas and often, locally, is very abundant. Apparently it is restricted to sandy soils on which pines have become dominant.

In many places the growth of pines is so dense that the ground is practically bare of vegetation, only scattering plants being found. In such places the ground is well carpeted by pine needles. This, probably, represents the typical condition of the climax pine forest, the presence of an abundance of herbs being due to a disturbance of typical conditions by passage of fire through the forest.

2. XERARCH SUCCESSION

Initial causes: A xerarch succession is one originating in a dry habitat. Such a habitat is to be found in Minnesota only in areas

where the surface is of solid rock, representing an extreme deficiency in water-content. The most extensive area of this kind is in northeastern Minnesota. Smaller areas occur along the south side of Lake of the Woods. These rocks are probably of igneous origin and belong to the Archean period. They consist of greenstones, quartzites, granites, gneisses, schists, and jasper variously intermingled. In northern and northeastern Minnesota, these Archean rocks have remained at the surface since the Archean period, while in other parts of the state except the southeastern the rocks of that period have been covered by sedimentary formations of subsequent periods. The passage of the glaciers during the Glacial period planed down the Archean rocks somewhat and left deposits of glacial till over some of them, but extensive areas still remain exposed. These constitute the bare areas for the initiation of xerarch succession.

Weathering of the exposed rock surface has contributed to the development of vegetation within that area. In some places the rocks are still as smooth as they were left after being worn down and polished by glacial action, and on these little or no vegetation is to be found. On others the surface of the rock has been disintegrated by weathering, in places to a depth of several inches, and in such places a dense covering of vegetation has developed.

A succession having its origin on rock and culminating in the *Pinus* climax association also shows a series of progressive stages. The stages of xerarch succession, however, are not as readily traced as those of the hydrarch and complete data are not yet at hand. From the available data of quadrats, transects, and field notes, the stages seem to be as follows:

(1) Crustose Lichen associes
(2) *Cladonia-Polytrichum* associes
(3) Herbaceous associes
(4) *Juniperus* associes
(5) *Pinus-Betula* associes
(6) *Pinus* association

(1) Crustose Lichen Associes

On bare hard rock owing to the extreme deficiency of water and the exposure to which they are subjected, crustose lichens alone are able to gain a foothold. Since these are able to grow during periods of wet weather and to remain in a state of dessication for an in-

definite time between periods favorable for growth, the conditions which are too adverse for other forms of plant life permit at least a certain amount of growth of lichen pioneers. "The crustaceous lichens furnish most of the species which first gain a footing on the rocks, and of these were found three or four species of *Placodium,* a half dozen or more *Lecanoras* as well as a large number of *Biatoras, Lecideas* and *Buellias.* Of the foliaceous lichens the *Umbilicarias* are most characteristically rock pioneers." (Fink, 1899: 221.) These might grow for hundreds of years before the establishment of any other plant form in that area. Rock surfaces may be found now which have not advanced beyond the crustose lichen stage, but it is not possible to say how soon or how long after the glacial period the invasion of such surfaces by the lichens began. A long-continued growth of crustose lichens on a rock surface, however, would tend to favor the invasion and establishment of other forms of plant life.

The formation of pools of water, even very small ones and of short duration, in shallow depressions of the rock surface, would provide a place to which algae and aquatic mosses might be carried and grow. This might happen repeatedly in the same place and would in time result in the accumulation of humus, and with the erosion of the rocks produce a small amount of soil in which other forms of plants could grow. Even without the invasion of algae or mosses, the accumulation of water in pools would carry in particles of rock that may have been loosened as the result of weathering, and in this way a small amount of soil be formed for the invasion of plants.

That algae and mosses may be carried to and live in pools of water on a solid rock surface can not be doubted. MacMillan (1897: 1017) mentions the occurrence on Windigo Island in Lake of the Woods of *Sphagnum cymbifolium* forming miniature peat bogs, of two or three feet in extent and two and a half inches deep, upon high wind-swept rocks.

When pools of water are invaded by aquatics, it results in the development of a miniature hydrarch succession. That this is true is readily apparent from the instance above cited. When such pools are of short duration, the hydrarch succession is so short that it may be neglected.

(2) *Cladonia-Polytrichum* Associes

The formation of soil in slight amounts takes place by the weathering and erosion of the rock surface. The weathering process is aided by the action of the crustose lichens which tend to erode the rock surface and to loosen particles of the rock. The disintegration of the rock and the addition of humus from the decay of lichens increases the water-content of the soil so formed. This increase in the water-content makes possible the establishment of larger lichens, such as *Cladonias,* and mosses.

Consocies: The plants typically represented in this associes are *Cladonia gracilis, C. rangiferina* and *Polytrichum commune.* One of the first lichens to appear after the crustose lichens is *Pannaria microphylla,* which may sometimes grow on quite firm rock but usually appears in more or less disintegrated areas. The large foliose *Peltigeras* and the fruticose *Cladonias* are the next to appear, commonly occurring with *Polytrichum.*

Among the *Cladonias, C. gracilis, C. fimbriata,* and such forms are most abundant in open and more exposed places. *C. rangiferina* may occur also in open places, but does not show the luxuriance of growth which is characteristic of it in more sheltered spots. The appearance of a few shrubs in crevices and pockets furnishes some protection from the sun and drying action of the wind, enabling *C. rangifernia* to make much better growth after the appearance of the shrubs.

These sometimes occur only in depressions in the rocks, since disintegrated particles of rock are carried into the depressions by rain, and such places are accordingly the only ones where conditions are suitable for the development of *Cladonia* and *Polytrichum.* In other places these plants form very extensive patches over the rock surface, often to a depth of several inches.

Secondary species: Other species of *Cladonia, Peltigera, Parmelia, Umbilicaria* and a few small mosses occur with the consocies.

(3) Herbaceous Associes

The further disintegration of rock surface by weathering, aided by the action of lichens and mosses and the addition of humus by their decay, forms a soil layer of greater or lesser thickness over the surface of the rock. The increase in the depth of soil and the increase in water-holding capacity by the addition of humus both

work together to make conditions suitable for the invasion of grasses and other herbaceous plants.

Consocies: This associes shows no dominance of any single species of plants nor even of a few species. Various species of grasses and herbs are to be found, but these are either scattered or a given species may show dominance over a very small area, i. e., by aggregation, it may form a family.

The following are the more representative plants of this stage:

Agrostis hiemalis	*Heuchera americana*
Arabis hirsuta	*Hieracium umbellatum*
Capnoides sempervirens	*Houstonia purpurea*
Carex canescens	*Muhlenbergia mexicana*
Chamaenerion angustifolium	*Panicum xanthophysum*
Diervilla lonicera	*Sibbaldia procumbens*
Euthamia graminifolia	*Solidago* sp.

Polypodium vulgare and *Dryopteris thelypteris* are found sometimes, especially in crevices. A large number of other plants might be named, since nearly all the plants of the region may grow in crevices and in pockets filled with soil.

(4) *Juniperus* Associes

The presence of the herbaceous associes, being usually poorly developed, does not have any evident reaction on the habitat in making it more favorable for the incoming of shrubs. However, clumps of grass and herbs might be of some value in protecting the young seedlings of shrubs from the intense light and heat of the sun, and thereby enable them to obtain a footing.

Consocies: *Juniperus communis* and *Sabina horizontalis* are the only dominants of this associes. Of these *J. communis* is the more abundant, often covering considerable areas.

Secondary species: *Taxus minor* occurs, but only occasionally. Many small deciduous shrubs are to be found also, the following being the most abundant:

Corylus americana	*Symphoricarpos racemosus*
Diervilla lonicera	*Vaccinium canadense*
Rhus rydbergii	*Vaccinium pennsylvanicum*
Rosa woodsii	

(5) *Pinus-Betula* Associes

The intensely xerophytic conditions of the habitat, due to the deficiency in water-content and to the great evaporation to which it is exposed in the bare rock condition, has been ameliorated gradually by continual weathering and by the addition of humus as the result of the decay of the pioneer lichens and plants of the successive developmental stages. Thus by the time that *Juniperus* and *Sabina* put in their appearance, a considerable depth of soil has been formed and the water-holding capacity of the soil has been increased markedly by the addition of humus. The habitat starting from intense xerophytism has approached to a mesophytic condition suitable for certain forms, at least, of trees. The presence of shrubs of the *Juniperus* associes further favors the establishment of trees by protecting the young seedlings from too intense evaporation and also by preventing evaporation from the soil in which they grow.

Consocies: The consocies are *Betula papyrifera* and *Pinus divaricata.* These may be intermixed, or either may be an exclusive dominant within small areas. Although the growth may appear dense when observed at a distance, a closer inspection reveals the fact that the plants are rather scattered, appearing only along crevices and in depressions where soil has accumulated more rapidly.

Secondary species: *Juniperus* and *Sabina* may persist indefinitely after the appearance of *Betula* and *Pinus divaricata,* occupying places less suitable for birches and pines or where the latter do not shade them too much. Other shrubs which grow better when partly shaded make their appearance with the advent of *Betula* and *Pinus.* The shrubs found most abundantly with this associes are:

Alnus incana	*Prunus virginiana*
Corylus rostrata	*Rhus rydbergii*
Diervilla lonicera	*Rosa acicularis*
Prunus pennsylvanica	*Rubus strigosus*

In addition to plants from the preceding associes, many of the shade-loving plants are to be found growing under the birches and pines. The more characteristic species are the following:

Actaea rubra	*Galium triflorum*
Aralia nudicaulis	*Lactuca canadensis*
Cornus canadensis	*Maianthemum canadense*
Fragaria virginiana	*Pteris aquilina*
Galium boreale	

In places where a few individuals of *P. divaricata* are grouped, the ground may be shaded to such an extent that very few plants are able to grow there. Patches of rock covered by *Cladonia rangiferina, C. gracilis,* other *Cladonias, Peltigera* and *Polytrichum,* or rocks with crustose lichens only are commonly to be found in the spaces between the tree growths.

(6) *Pinus* Association

The appearance of the *Juniperus* associes and the subsequent *Betula-Pinus* associes brings about a more rapid accumulation of humus, due to the increase in the number and size of individuals able to inhabit the area. The weathering processes still continue to break down the rocks and increase the amount of soil. All changes, accordingly, work to bring the habitat to more nearly mesophytic conditions. In the spaces between birch and jack pines and more or less shaded and protected by them, the invading pines of the *Pinus* association find suitable conditions for development.

Consocies: The consocies of the climax forest here as in the hydrarch succession consists of two species of pines, *P. resinosa* and *P. strobus.* No difference is to be found in the climax of the xerarch succession as compared with that of the hydrarch, except that the presence of certain secondary species may indicate along which line the succession has been.

Secondary species: As undershrubs of this associes are found:

Corylus rostrata	*Rosa acicularis*
Diervilla lonicera	*Rubus strigosus*
Lonicera hirsuta	*Vaccinium canadense*
Prunus pennsylvanica	*Vaccinicum pennsylvanicum*
Prunus virginiana	

The presence of patches of bare rock or of lichen-covered rock, which have persisted throughout the stages leading up to the climax, breaks up the climax somewhat, and allows more under-vegetation than might otherwise be possible. The herbaceous layer consists of *Aralia, Cornus, Maianthemum, Chimaphila* and *Pyrola* as characteristic species. The fact that in an area of even a few acres, hydrarch and xerarch successions occur side by side and, further, that these have been disturbed during their development, perhaps repeatedly, makes it difficult to state with assurance whether certain species are characteristic of normal primary succession or

whether they have appeared as the result of the initiation of more or less extensive secondary successions. However this may be, the general sequence of events in the succession seems quite clear.

II. Secondary Succession

Initial Causes: Any cause that destroys the existing vegetation of an area may initiate a secondary succession. Such causes may be changes in the physiography of a region, climatic or edaphic changes, or changes resulting from the action of biotic agents. None but biotic agents apparently cause secondary successions in Minnesota, except to the extent that forest fires, for example, may be shown to have been started by lightning.

Secondary successions may begin at any point after the pioneer stage and before the final climax. The point at which the succession does begin is determined by the extent to which the water-content is affected by the disturbance of the habitat. A secondary succession may be a very local one, such as might be produced by a windfall or by the formation of a small pond, or it may cover an area of hundreds of square miles. In a large area the water-content of the habitat is apt to be affected more profoundly, which would cause the secondary succession to begin at an earlier or lower stage. Secondary successions may be classified as follows:

1. Flood succession
2. Burn or clearing succession

1. THE FLOOD SUCCESSION

As indicated by the name, this is a succession due to the flooding of an area from any cause whatsoever. The two principal agents in causing secondary succession by flooding in northern Minnesota are man and beavers. The flooding may be over a very restricted area or over an extensive one, in either case causing a more or less complete hydrarch succession. If over an extensive area, the depth of water is apt to become sufficient to initiate a primary succession beginning with *Chara* and other plants of that associes as already described (page 337).

In making reservoirs of Gull, Leech and Winnebegoshish lakes, the water-level has been raised several feet over extensive areas surrounding these lakes and along rivers tributary to them. In the same way the building of dams in rivers to obtain power for light-

ing or for the operation of machinery has resulted in the initiation or secondary succession along the rivers affected for a distance of several miles above the dams. Man has been the agent in causing these successions. Beavers, by building dams across streams, cause a flooding of areas along the streams for some distance above the dams. The areas affected by beaver dams, however, are usually small, although such areas are found quite often.

The topography of a region determines in a large measure the extent to which an area may be affected by flooding and consequently determines the stages at which secondary succession will begin. If the shore of a lake or banks of a stream are high and steep, a rise of several feet in the water-level may produce no very evident effect. On the other hand, if a lake or river is bordered by marsh or swamp, a rise of a foot or even of a few inches may effect the vegetation to a marked extent. The shores of Leech and Winnebegoshish lakes are diverse in character, but for the most part are sufficiently high and steep so that the raising of the water-level by the conversion of the lakes into reservoirs has not affected succession except in rather local areas. Leech Lake furnishes the best examples of succession.

Leech Lake, on the east side, between Leech Lake River and Boy River and south about an equal distance, is bordered by a tamarack swamp. Similar swamps occur at the north end of Sucker Bay, on the west side of the same bay and at the north end of Steamboat Bay and along Steamboat River. The swamps also form a zone along streams tributary to Leech Lake at the places named.

The rise of the water-level has resulted in the killing of the tamaracks in the areas above named, except along the margins. As a result, the *Larix-Picea* associes has been replaced by a *Carex-Calamagrostis* associes, which is similar in all its characteristic features to the *Carex* associes as described under primary succession (page 340), except that *Calamagrostis canadensis* and *C. hyperborea* become codominants with the species of *Carex*.

In the deeper water bordering the zone of *Carex-Calamagrostis*, *Zizania* and *Phragmites* occur. Along with these, especially near the mouth of Boy River, *Equisetum fluviatile* appears conspicuously as a socies, often dominating quite extensive areas. *Scirpus* and *Typha* were absent from nearly all of the areas observed.

In deeper water just outside the *Zizania-Phragmites* zone, *Castalia, Nymphaea* and *Potamogeton* were sometimes found. Their

presence or absence is to be explained by the topography and nature of the lake bottom.

Young trees of *Larix, Betula pumila, Salix candida, S. petiolaris* and others were found as invaders along the shoreward edge of the *Carex-Calamagrostis* zone of the secondary succession. *Betula pumila* and *Salix candida* usually occurred farthest out. More to the shoreward, *Larix* occurred, and with it or sometimes preceding it were found *Ledum* and *Cornus stolonifera.* With the invasion and establishment of *Larix* and *Picea,* the original conditions are restored.

2. BURN OR CLEARING SUCCESSION

a. In the Climax Forest

The removal of the climax forest affects the water-content of the soil to a greater or lesser extent by drying the soil, first by the passage of fire, and second by exposure to the action of sun and wind, in case of either burning or clearing. The light relations are greatly changed also, and many of the characteristic plants of the ground layer in the forest disappear, since they are unable to endure the intense light and increased transpiration attendant thereon.

Although initiated by distinctly different causes, the course of succession is essentially or, sometimes, precisely the same, the difference being of degree and not of kind. Fires, particularly if of great extent and fierceness, may affect an area more seriously in that all the under-vegetation and even the leaf-mould on the surface of the ground may be burned and removed completely. Seeds and perennial underground parts are thus destroyed and succession must begin anew. If such a burn occurs in a region with rock outcrop, the succession may be a primary one beginning with crustose lichens, or a secondary one beginning with foliose and fruticose lichens. Clearing alone would never bring this about. In areas of sand, clay, loam, or mixtures of these, the deeper-lying underground parts and seeds would not be destroyed and would enable the succession to begin at a later stage. These two causes often work together, as where the brush and slashings are burned after the valuable timber has been removed. Fires of such kind are less destructive and allow succession to begin at a later stage than would otherwise happen.

Windfalls, whether affecting a considerable number of trees as a group or only a single individual, give rise to secondary successions. These are to be considered with cleared successions from

which they differ in no essential respect. The fact that the clearing has been brought about by the action of a biotic agency in one case and by a natural force in another is of no significance.

The extent of the area cleared or burned affects the succession by modifying the rate of migration into the burn or clearing. This is particularly true in case of destructive fires where seeds or propagules on or near the surface are killed by the heat of the fire. Over large burned or cleared areas, invasion would be greatest near the edge because of the greater number of disseminules carried by wind from the surrounding forest. Light disseminules carried by wind could invade farther and in greater number than those with heavy seeds or fruits. *Populus* and *Betula* could invade an area more rapidly, for example, than *Pinus*.

Since most of the area covered by the pine forest has been cut over in lumbering and also since most of it has been burned over at one time or another, in some places several times, the pine forest as we find it now is largely developed by secondary succession. Thus the consideration of secondary succession due to lumbering and burning is of much importance. Except for areas in which the climax pine forest has developed through hydrarch or xerarch successions, the study of succession in other areas is wholly a study of secondary succession.

Since fire is more destructive to the vegetation of an area and therefore will cause secondary succession to begin at an earlier or lower stage, the initiation of secondary succession as a result of burning will be treated first. The successive stages will be taken in order, the cause of initiation at any particular stage being indicated in the discussion of that stage.

Very destructive fires may not only remove the existing vegetation of a region, but also destroy the humus that may have accumulated on the ground and with it all the seeds and propagules of every kind so that succession must begin at a very early stage. In areas of rock where only a shallow layer of humus exists, without the presence of soil, a fire may cause the initiation of a primary succession beginning with crustose lichens. The lowest stage, however, in which a secondary succession can begin is with the *Cladonia-Polytrichum* associes.

(1) The Lichen Associes

When fire sweeps over a region destroying the forest and the

forest undergrowth, various species of *Cladonia,* especially *C. gracilis, C. cristatella, C. fimbriata, C. pyxidata* and *C. verticillata,* appear on the partly burned stumps and half-buried trunks and branches of trees. Scattered lichens and mosses may occur also over the surface of the ground, which is otherwise bare. Successions beginning with this stage, however, are rather rare, owing to the ease with which herbaceous or woody invaders may enter.

(2) THE HERBACEOUS ASSOCIES

The usual point at which secondary succession begins after a fire is with the appearance of herbs and grasses. In the northern and northeastern part of the state, *Chamaenerion* is often the dominant species. With this in greater or lesser abundance are to be found species of *Aster* and *Solidago.* In some places, indeed, the latter genera vie with *Chamaenerion* as to abundance. Grasses such as *Agrostis hiemalis, Muhlenbergia mexicana, Panicum xanthophysum, Agropyron tenerum,* and *Elymus canadensis* are nearly always present. *Agrostis* is usually the most abundant.

Other species usually present with the above are:

Anaphalis margaritacea	*Leptilon canadense*
Carduus altissimus	*Onagra biennis*
Lactuca sp.	*Pteris aquilina*

In places where the soil is very sandy, the succession shows considerable difference from the above. In such places the secondary succession after fire or clearing begins with grasses. *Danthonia spicata* is often dominant, occurring alone or with an intermixture of *Fesuca ovina.* In places not occupied by grass, *Arctostaphylos uva-ursi* is often found, at times spreading over quite extensive patches. Other plants occurring with these are the following:

Antennaria canadensis	*Oryzopsis micrantha*
Aster laevis	*Panicum xanthophysum*
Lacinaria scariosa	*Solidago nemoralis*
Lechea stricta	

A third variation in sequence is found to exist. This, too, is found in sandy soil and near the southern limit of the pine forest approaching the prairie. Here a burned or cleared area soon passes into an *Andropogon* socies with *A. furcatus* as the dominant species. *A. scoparius, Stipa spartea, Agropyron caninum* and *Poa nemoralis*

are usually found with *A. furcatus,* but not very abundantly. Apparently it happens that *Danthonia* and various herbs as described above come in first, only to be replaced by *Andropogon,* which crowds out the other plants. Other secondary species occurring with *A. furcatus* are the following:

Achillea lanulosa	*Campanula rotundifolia*
Agastache anethiodora	*Equisetum hiemale*
Agrostis hiemalis	*Erigeron ramosus*
Artemisia caudata	*Helianthemum canadense*
Aster laevis	*Hieracium umbellatum*
Bromus Kalmii	*Lacinaria scariosa*

When an area has been plowed after clearing and then abandoned, it grows up for a few years to ruderals and semi-ruderals, such as *Leptilon canadense, Chenopodium album, Amaranthus retroflexus, A. graecizans, Onagra biennis, Achillea lanulosa, Erigeron ramosus* and such grasses as *Agropyron tenerum, A. caninum, Elymus canadensis* and *Agrostis alba.* The grasses tend to increase and crowd out the weeds, but before the grasses gain control the area is usually invaded by shrubs and trees, which become dominant at the expense of both weeds and grasses.

(3) *Corylus-Rubus* Associes

Following fires of less intensity and following the removal of the forest by clearing, secondary succession may begin with an associes of *Rubus strigosus* and *Corylus americana.* This is more often true after clearing than after burning, since the former does not destroy any under-shrubs which may be present. In a secondary succession beginning with one of the lower stages, the shrubs invade the herbaceous associes and soon become dominant by crowding out the herbs. Usually the invasion begins with the appearance of *Diervilla lonicera* in the herbaceous associes, to be followed soon by *Corylus* and *Rubus.* In the area near Ely where the surface is largely of rock, *Comptonia peregrina, Pteris aquilina* and *Diervilla lonicera* with *Chamaenerion* and *Aster* constitute a stage prior to the appearance of the *Rubus-Corylus* associes.

Consocies: The species most often found as dominants of this associes, as indicated in the name, are *Rubus strigosus* and *Corylus americana. Alnus crispa* and *Prunus pennsylvanica* may be found as consocies, or in places may replace one or both of the usual con-

socies. *Alnus,* however, usually replaces *Corylus* and *Rubus* only in areas where the water-content of the soil is greater.

Secondary species: In many places, *Prunus pennsylvanica* is less abundant and must rank as a secondary species. *Alnus incana* occurs in some areas also. In rather moister soil and often with *Alnus incana, Corylus rostrata, Salix discolor* and sometimes other willows occur abundantly. The usual secondary species of this associes are:

Anaphalis margaritacea	*Lacinaria scariosa*
Aster laevis	*Onagra biennis*
Chamaenerion angustifolium	*Pteris aquilina*
	Solidago canadensis
Diervilla lonicera	*Solidago nemoralis*

Many other species are to be found, viz., plants of the forest which have persisted after its removal or destruction and patches of grass with their attendant secondary species that have not been replaced by the shrubs of this associes.

(4) *Populus-Pinus divaricata* ASSOCIES

The presence of shrubs of the *Corylus-Rubus* associes serves to keep the soil of the habitat moist and protect the seedlings by shading them, and thereby enables the trees of the associes to become established.

Some notable variations in this sequence may occur. In some cases *Pinus divaricata* and *Populus tremuloides* may invade and become dominant directly following the removal of the climax forest without the appearance of the usual antecedent stages. This is often found to occur in the area of sand and gravel outwash in southern Beltrami, parts of Cass, Hubbard, Wadena, Becker and Crow Wing Counties, particularly with reference to *Pinus divaricata.* It may occur also in other districts, especially in places where the water-content of the soil is high. *Populus tremuloides* is apt to become an early dominant in such places.

It has been observed, in some places, that *Andropogon furcatus* may become the dominant after burning or clearing, and that *Pinus divaricata* may invade the grass directly without a previous development of shrubs. Sometimes *P. divaricata* alone invades, at other

times it may be accompanied by *Betula papyrifera* or by *Quercus coccinea* or both.

Consocies: The usual consocies are *Populus tremuloides, Pinus divaricata* and *Betula papyrifera.* To these *Quercus coccinea* may be added for certain areas. Any two or more of these may form a mixture, or in other places the associes may be represented by but one of its consocies.

In the region of surface rock, near Tower and Ely, *Betula papyrifera* often occurs in socies. The same may be said of *P. divaricata* in the same area, but more particularly this is true of *P. divaricata* in areas of outwash sand and gravel above mentioned. In Crow Wing County, *Quercus coccinea* occurs as a consocies. This has not been found to apply elsewhere. In areas of greater water-content in the soil, socies of *P. tremuloides* may be found.

Secondary species: Other species of *Populus,* viz.: *P. grandidentata* and *P. balsamifera,* usually occur with *P. tremuloides,* but not in sufficient abundance to rank as consocies. Colonies or socies of *P. grandidentata* may occur sometimes. *Quercus coccinea* is present in many places.

A number of shrubs are characteristic of this associes in secondary succession:

Acer spicatum	*Prunus virginiana*
Alnus incana	*Ribes americanum*
Cornus stolonifera	*Rosa acicularis*
Corylus rostrata	*Rosa blanda*
Diervilla lonicera	*Rubus strigosus*
Lonicera oblongifolia	*Vaccinium canadense*
Prunus pennsylvanica	*Vaccinium pennsylvanicum*

In some areas *Alnus crispa* may be found with *A. incana. Lonicera hirsuta, Ribes gracile* and *Rubus allegheniensis* occur occasionally.

The herbs of this associes are numerous. The following are usually present:

Anemone quinquefolia	*Chimaphila umbellata*
Aralia nudicaulis	*Cornus canadensis*
Aster cordifolius	*Falcata comosa*
Aster laevis	*Fragaria virginiana*
Aster macrophyllus	*Gaultheria procumbens*

Lathyrus venosus	*Pteris aquilina*
Lycopodium clavatum	*Pyrola americana*
Lycopodium obscurum	*Pyrola secunda*
Maianthemum canadense	*Rubus triflorus*
Oryzopsis asperifolia	*Viola conspersa*

Arctostaphylos uva-ursi and *Danthonia spicata* are present, usually in abundance, *Arctostaphylos* forming broad mats over the surface of the ground. There were found only in the area of sand and gravel outwash, and were not noted elsewhere. *Lycopodium complanatum* occurs in the northeastern part of the state, but has not been observed at other places.

The following may be present, but usually only as scattered individuals or in restricted areas: *Apocynum androsaemifolium, Clintonia borealis, Comandra umbellata, Habenaria orbiculata, Hepatica triloba* and *Lathyrus ochroleucus*.

Pinus resinosa and *P. strobus* of the climax association begin to invade this associes, especially in any gaps that occur due to windfalls or to the death of one or a few trees from any cause. *Pinus divaricata* and *Populus tremuloides* are both short-lived, the wood of both is brittle, and the trees are easily broken off by wind, so that the opportunity for invasion by the long-lived pines of the climax forest is soon presented. The composition of the climax forest and its characteristic secondary species have already been discussed (page 345) and need not be repeated here.

b. Secondary Succession in the Larix-Picea Subclimax

Although the *Larix-Picea* associes represents only a stage in the development of the climax pine forest, it is a stage which often persists indefinitely as a subclimax on account of the great differences in the habitat as compared with that of the climax pine forest. The very different habitat conditions result in marked differences in the vegetation and in a difference in the sequence of successional stages, which makes it necessary to treat secondary successions in tamarack swamps under a special heading.

The causes work in the same way and may operate singly or together, as indicated elsewhere. Fire as the more destructive agent affects the habitat more profoundly and causes succession to begin at a lower stage. This is especially true if burning occurs during a

dry season when the *Sphagnum* surface is partly dry. At such times burning may result in killing out the *Sphagnum* and in the initiation of a secondary succession beginning with *Carex-Calamagrostis*. The sequence of stages after the appearance of *Carex-Calamagrostis* up to *Larix-Picea* is essentially that of primary succession. In some instances *Populus* may invade directly after a fire so that a dense growth of seedling poplars is the dominant vegetation.

When a tamarack swamp is drained and afterward burned, the succession begins usually with the *Carex-Calamagrostis* associes. As a result of the combined draining and burning, all the characteristic plants of the swamp disappear. The water-content of the habitat is still high but much less than if Sphagnum were present. The disappearance of *Sphagnum, Larix* and other swamp species permits the invasion of *Carex* and *Calamagrostis,* so that the *Larix-Picea* stage comes to be replaced by the associes of *Carex-Calamagrostis* as the first stage of secondary succession initiated by draining and burning. If the area affected be mowed or burned over each year, it may be kept indefinitely in this stage and valuable hay meadows result. If the swamp be kept drained but not mowed nor burned over, a secondary succession culminating in climax pine forest will ultimately result.

In such a case the *Carex-Calamagrostis* associes is invaded first by *Betula pumila, Salix petiolaris,* soon followed by *Salix bebbii, S. discolor, Cornus stolonifera* and *Alnus incana.* As a result of the invasion of these, the plants of the *Carex-Calamagrostis* associes are killed out. The swamp gradually fills up by the washing in of soil around the edge, aided by the accumulation of humus from the decay of dead vegetation. The process of filling reduces the water-content of the soil and permits the invasion of *Populus, Abies, Betula* and sometimes *Fraxinus nigra.* The invasion proceeds from the edge, gradually encroaching on the swamp. After a time the associes of *Abies-Betula* as described on page 344 becomes established. This is later invaded by pines as already described in normal primary succession. The successional stages of secondary succession in drained swamps from the initial stage up to the climax pines appear more rapidly than in normal primary succession, but in stages common to both the composition of a common associes and the secondary species present in that associes are essentially alike.

The removal of the dominant *Larix-Picea* layer without subse-

quent burning does not seriously affect the successional sequence since the water relations of the habitat remain essentially unchanged. The most marked effects are in the changed light relations and increased exposure to evaporation. These changes may result in the disappearance of some of the shade-loving plants.

In extensive swamp areas where filling from the edge can not alter the general conditions of the swamp, the effect of clearing is to permit the development of the bog shrubs which had been suppressed by the tamarack and spruce and consequently in the reestablishment of an associes of *Ledum, Andromeda* and *Chamaedaphne.* Usually the clearing is not complete, a greater or lesser number of young tamarack and spruce being left. These now develop, and with the appearance of new tamarack and spruce, the original *Larix-Picea* associes soon becomes dominant again.

In small swamps and in a zone along the edge of larger swamps where the soil is built up more as the result of filling in, an associes of *Alnus incana, Cornus stolonifera* and species of *Salix* appear after the removal of *Larix* and *Picea. Betula pumila, Lonicera oblongifolia, Ribes hudsonianum* and *R. triste* occur more or less abundantly with these.

Windthrows are to be regarded as miniature clearings. In a *Larix-Picea* swamp, when a windfall occurs, its place is invaded at once by *Larix* and *Picea* or by either of these alone, which results in keeping the area indefinitely in the same developmental stage in spite of the prevalence of windfalls. This applies in deep swamps where *Sphagnum* is abundantly developed.

In swamps that are more nearly filled up and where in consequence *Sphagnum* makes little or no growth, *Picea, Thuja, Abies, Betula* and *Populus* appear in the places left vacant by windthrows. *Alnus incana, Salix discolor* and *Cornus stolonifera* often come in also, but these are later replaced by the trees named above. As the swamp fills up, an *Abies-Betula* associes becomes established to be succeeded finally by the climax pine forest as the process of filling is carried still further.

A *Larix-Picea* swamp, if drained and not disturbed by clearing or burning, gradually fills up, thereby reducing the water-content of the soil. With the draining away of the water and filling up, *Sphagnum* disappears. As the filling up proceeds, *Larix* dies out, *Picea* and *Thuja* taking its place. In time *Abies balsamea, Betula*

papyrifera and *Fraxinus nigra* come in also, the invasion proceeding from the edge where filling occurs most rapidly. As a result of drainage not complicated by the introduction of other factors, the normal primary succession from *Larix-Picea* through the *Abies-Betula* associes to the climax pine occurs. Thus it appears that drainage alone merely accelerates the normal primary succession.

ACER-TILIA ASSOCIATION

I. Primary Succession

1. HYDRARCH SUCCESSION

Initial causes: The formation of bodies of water of sufficient size and depth to completely denude affected areas provides conditions for the initiation of primary succession. The origin of lakes in Minnesota has been indicated briefly under "Initial Causes" in the discussion of primary succession in the area of the pine forest climax.

A succession having its origin in water and culminating in the *Acer-Tilia* climax association shows a series of stages as follows:

(1) *Chara-Philotria* Associes
(2) *Castalia-Nymphae* Associes
(3) *Scirpus-Zizania* Associes
(4) *Carex* Associes
(5) *Larix-Picea* Associes
(6) *Populus-Betula* Associes
(7) *Acer-Tilia* Association

A variation of this sequence may occur by the failure of the *Larix-Picea* associes to develop between the *Carex* associes and the climax association. This is true particularly where the land rises rather abruptly from a swamp or meadow, resulting in a sudden drop in the water-content of the soil. In some instances the *Larix-Picea* associes is found to be preceded by a *Chamaedaphne-Andromeda* associes, while in other instances the latter does not appear. Which of these variations is to be regarded as the rule and which the exception it is not possible to state from evidence now available. When more places in the deciduous belt have been studied a definite answer can be made with reference to this point.

Since the stages in the development of the deciduous forest climax in many respects are the same as the corresponding stages in the development of the pine forest climax, the discussion will be restricted to the pointing out of differences, when such exist.

(1) *Chara-Philotria* Associes

As to causes, consocies and secondary species the initial stage here is the same as the initial stage leading up to the pine forest climax which is discussed on page 337.

(2) *Castalia-Nymphaea* Associes

This associes is similar to the corresponding associes in the development of the pine forest climax through hydrarch succession. (See discussion on page 337.)

(3) *Scirpus-Zizania* Associes

See discussion of corresponding associes on page 338 from which this shows no essential variation. A striking feature of this associes as found in Star and Dead lakes in Otter Tail County is the very extensive area of *Zizania* which completely filled some of the long shallow arms of these lakes. From shore it had the appearance of meadows of *Zizania,* though with a rowboat or canoe one could go anywhere through it. Shores exposed to severe wave-action or to the action of wind-driven ice as the ice breaks up in the spring are free of *Zizania* and usually also of *Scirpus, Typha* and others of this associes.

(4) *Carex* Associes

Causes: The filling up of lakes or ponds by the washing-in of eroded material from the sides and by the accumulation of decayed plant remains results in the reduction of the water-level along the shore. This permits the invasion of plants of this associes.

Consocies: The following are typical dominants of this associes:

Carex aquatilis
Carex diandra
Carex filiformis
Carex lanuginosa
Carex trichocarpa

Carex aquatilis and *C. trichocarpa* are less prominent than in the corresponding associes of hydrarch succession culminating in the climax pine forest, their place being taken usually by *C. filiformis, C. lanuginosa* and *C. diandra.* In many places the associes occupies only a narrow zone while in others it is more extensive. As in the development of the Pinus association so here the Carex associes may follow directly after the *Castalia-Nymphaea* stage with only a sparse growth of *Zizania* or *Zizania* and *Scirpus* intervening, or these may be entirely absent.

Secondary species: The following species of herbs are characteristic:

Alsine longifolia	*Lycopus lucidus*
Aster paniculatus	*Mentha canadensis*
Campanula aparinoides	*Menyanthes trifolia*
Comarum palustre	*Naumbergia thyrsiflora*
Dryopteris thelypteris	*Scutellaria galericulata*
Galium trifidum	*Sium cicutaefolium*

(5) *Larix-Picea* Associes

Causes: The appearance of *Sphagnum* as described on pages 341 and 342 may lead up to this associes, following the *Chamaedaphne-Andromeda* associes as in the development of the climax pine forest. This has been observed in some places, but in others *Larix* may appear without being preceded by the *Chamaedaphne-Andromeda* associes. That this procedure is not to be regarded as normal but rather as a departure from it due to draining, burning, clearing or other disturbance initiating a secondary succession, seems probable. When more evidence becomes available by the study of development in other places in the deciduous forest region, this point will be decided.

Consocies: The associes consists typically of two consocies, *Larix laricina* and *Picea mariana*.

Larix ranges much farther southward than Picea, so that the former is often the only representative of the associes.

Secondary species: The following shrubs usually occur in this associes:

Betula pumila	*Salix cordata*
Cornus stolonifera	*Salix discolor*
Salix bebbii	*Salix petiolaris*
Salix candida	

Betula pumila and *Salix candida* are often the first to invade the *Carex* associes and sometimes form a scattering zone between it and the *Larix* zone. The herbs of this stage are the consocies of the *Carex* stage with its characteristic secondary species, which usually persist as relicts in the *Larix-Picea* associes.

(6) *Populus-Betula* Associes

Causes: Further filling in along the edge of swamps by wash-

ing in of eroded material and by the accumulation of organic matter from decay of plant bodies results in a reduction in the water-content. The development of the *Larix-Picea* associes results in a reduction or in the more or less complete disappearance of grasses and sedges. Where the tamaracks are dying out, or in vacant places resulting from windthrows, *Populus* and *Betula* are able to invade and in time become established.

Consocies: The species usually appearing as consocies are: *Betula papyrifera, Populus tremuloides, P. grandidentata,* and *P. balsamifera. Fraxinus nigra* is often found with these but not in sufficient numbers to rank as a consocies. *P. tremuloides* and *P. grandidentata* are usually the most abundant, but in places may not appear at all, the associes being represented in such places by *Betula.*

Secondary species: The undergrowth consists of the following shrubs:

Cornus stolonifera	*Ribes americanum*
Corylus americana	*Rosa blanda*
Parthenicissus quinquefolia	*Rubus strigosus*

The following are the most abundant plants of the ground layer:

Aralia nudicaulis	*Galium triflorum*
Aster macrophyllus	*Maianthemum canadense*
Carex longirostris	*Oryzopsis asperifolia*
Circaea alpina	*Phryma leptostachya*
Circaea lutetiana	*Pyrola americana*
Cystopteris fragilis	*Ranunculus abortivus*
Dryopteris cristata	*Rubus triflorus*
Erigeron philadelphicus	*Smilacina stellata*
Festuca nutans	*Viola conspersa*
Fragaria americana	*Viola papilionacea*

(7) *Acer-Tilia* Association

Causes: The further filling of the low area by the washing in of soil and by the accumulation of decayed plant-remains brings about a reduction in the water-content of the soil. The habitat has now become mesophytic in character. The invasion of the *Populus-Betula* associes by the species of the climax forest occurs when the poplars or birches die out as the result of competition or when windfalls occur. The fact that *Acer, Tilia* and others of this as-

socies are longer-lived than *Populus* and *Betula* enables them to crowd out the latter in competition.

Consocies: This association is represented by the following species:

Acer saccharum	*Quercus rubra*
Fraxinus lanceolata	*Tilia americana*
Quercus macrocarpa	*Ulmus americana*

These are usually well mixed, and the exclusive dominance of any one of them is rather exceptional, although within small areas *Acer, Tilia* or *Quercus* may be present in far greater numbers than any other of the usual consocies. In very sandy soil and further northward, *Acer* disappears and species of *Quercus* become more abundant.

Secondary species: In the upper or dominant layer may be found with the consocies occasional trees of *Betula papyrifera, B. lutea, Populus deltoides, P. balsamifera* and *Ulmus fulva*. Some of these, such as *Betula* and *Populus,* have persisted from the preceding associes.

The usual small trees and shrubs of this associes are:

Acer spicatum	*Rhus rydbergii*
Amelanchier canadensis	*Ribes americanum*
Cornus stolonifera	*Ribes cynosbati*
Corylus americana	*Ribes gracile*
Crataegus macrantha	*Rosa blanda*
Crataegus punctata	*Rubus strigosus*
Crataegus rotundifolia	*Symphoricarpos occidentalis*
Ostrya virginica	*Viburnum opulus*
Parthenocissus quinquefolia	*Vitis vulpina*
Prunus americana	*Xanthoxylum americanum*
Prunus virginiana	

Forming thickets along the edge of the woods, *Prunus americana, P. virginiana, Rhus glabra, R. hirta, Corylus americana, Cornus stolonifera, C. paniculata, Ribes gracile, Rosa blanda, Rubus strigosus* and *Symphoricarpos occidentalis* occur commonly. *Prunus. Rhus* and *Corylus* usually form families or colonies. The others usually occur in mixtures and rarely form families or colonies. In

some places all of these may be scattered quite promiscuously. *Ceanothus ovatus* occurs abundantly in a few localities.

The following are the characteristic plants of the ground layer in the *Acer-Tilia* climax forest:

Actaea rubra	*Maianthemum canadense*
Anemone quinquefolia	*Phlox divaricata*
Aquilegia canadensis	*Polygonatum commutatum*
Aralia nudicaulis	*Rubus triflorus*
Arisaema triphyllum	*Sanguinaria canadensis*
Aster cordifolius	*Sanicula marylandica*
Aster macrophyllus	*Smilacina racemosa*
Bicuculla canadensis	*Smilacina stellata*
Bicuculla cucullaria	*Smilax herbacea*
Carex laxiflora	*Syndesmon thalictroides*
Carex longirostris	*Thalictrum dasycarpum*
Erigeron philadelphicus	*Thalictrum dioicum*
Fragaria americana	*Trillium cernuum*
Fragaria virginiana	*Urticastrum divaricatum*
Galium aparine	*Uvularia grandiflora*
Galium triflorum	*Viola papilionacea*
Hepatica triloba	*Viola pubescens*
Hydrophyllum virginianum	*Viola sororia*
Lonicera dioica	

The following may be found occasionally:

Aralia racemosa	*Orchis spectabilis*
Caulophyllum thalictroides	*Osmunda cinnamomea*
Dryopteris cristata	*Osmunda claytoniana*
Meibomia grandiflora	*Osmunda regalis*
Oakesia sessiliflora	*Polygonatum biflorum*
Onoclea sensibilis	

In low places, *Urtica gracilis, Urticastrum divaricatum* and *Matteuccia struthiopteris* may occur in dense colonies or only as scattered individuals.

II. Secondary Succession

Secondary succession in the climax deciduous forest region as in the pine forest climax are of two kinds, namely:

1. Flood succession
2. Burn or clearing succession

1. FLOOD SUCCESSION

The survey party has made no specific study of secondary succession resulting from flooding by lakes or streams in any of the deciduous areas. The general course of development may be indicated, however, leaving the discussion of details for a later report. Flood successions occur most frequently along river valleys and are due to silting up of rivers, which ponds the water above the place where silting occurs or to the formation of small lakes on the flood plain of a river during a period of overflow. Usually the water is sufficiently shallow so that the succession can begin with the appearance of *Typha, Scirpus, Phragmites* and often also *Spartina cynosuroides*. *Phragmites* and *Spartina* grow in shallower water than *Typha* or *Scirpus* so that the latter are usually most abundant in shallow lakes on flood plains. These are followed by species of *Carex* of which *C. trichocarpa* is probably most abundant. With it are usually to be found *Calamagrostis, Panicularia americana* and *Spartina*. As filling of the flooded area proceeds, species of *Salix* and *Populus* are able to invade and still later *Acer negundo,* and finally the climax dominants *Ulmus, Quercus, Tilia,* and *Acer saccharum* become established. If flooding is recurrent the succession may be held in the *Typha-Phragmites* stage, or if the depth of water is less, in the *Carex-Calamagrostis* stage.

2. BURN OR CLEARING SUCCESSION

a. In the Climax Forest

Causes: The removal of the climax forest by burning or clearing is the fundamental cause of the initiation of secondary succession. Either of these causes results in a drier habitat, since the soil is directly exposed to the drying action of sun and wind. Plants growing in such areas are likewise exposed to drying action of sun and wind, and in consequence only those which are structurally adapted to prevent or check transpiration, or which are capable of physiological adjustment to such conditions, are able to grow in the altered environment. The changed light relation, since it affects the plants by affecting transpiration and by increasing the evaporation of water from the soil, is an important consideration.

The secondary succession which follows clearings of upland deciduous forests consists of the following stages:

(1) *Andropogon-Stipa* Associes
(2) *Corylus-Rubus* Associes
(3) *Populus-Betula* Associes
(4) *Acer-Tilia* Association

(1) *Andropogon-Stipa* Associes

Fires in deciduous forests rarely gain headway as under pines. However, where a deciduous forest joins a prairie or a meadow which is burned occasionally or annually, the fire tends to destroy the edge of the forest, and in time the climax forest may be replaced by the prairie, which can maintain itself if burning continues.

Consocies: In parts of Meeker, Otter Tail and Crow Wing counties, small areas of prairie often join tracts of the climax forest. In such areas *Andropogon furcatus* and *Stipa spartea* are the consocies. *Andropogon* is generally much more abundant than *Stipa,* the latter occurring as families or colonies in the *Andropogon* areas.

Secondary species: Other grasses such as *Andropogon scoparius, Agropyrum caninum, Agrostis hiemalis* and *Koeleria cristata* are to be found usually with the consocies. The following herbs are characteristic: *Campanula rotundifolia, Achillea lanulosa, Phlox pilosa, Heuchera hispida, Petalostemon candidus, Solidago nemoralis* and *S. missouriensis.*

When clearings are cultivated for a time and abandoned, the succession differs from that just described. Cultivation destroys all the under-shrubs and the succession must begin at a lower stage. This stage is an herbaceous associes of the uncultivated clearings. Abandoned fields are soon covered with weeds and grasses which are more or less abundant in poorly cultivated fields. The herbaceous associes of the deciduous area in main is similar to that of the coniferous area (see page 349). However, where the deciduous clearing is near the prairie more of the prairie species invade.

(2) *Corylus-Rubus* Associes

The *Andropogon-Stipa* associes will be maintained as long as the fires recur with sufficient frequency to kill out any invading shrubs or trees, as for example when an area is burned annually. Prairie that has developed as the result of repeated burning of an

area may be invaded by *Corylus, Rubus, Rhus* and *Rosa*. This occurs always when a prairie area near woodland ceases to be burned repeatedly, so that the shrubs become established. The covering of grasses and herbs protects the seedlings of the shrubs which soon grow up. As these increase in number by the appearance of other seedlings and by sprouts from roots of older plants, the grasses are killed out and the typical shrub associes takes its place. Clearing alone usually results in the initiation of a secondary succession beginning with this stage. When the forest is removed and the land left uncultivated, the shrubs which have been suppressed because of shade can now develop. *Corylus* soon becomes the dominant shrub. *Rubus,* if not present in the climax forest, is one of the earliest invaders.

Consocies: *Corylus americana* and *Rubus strigosus* are the usual consocies. *Rhus hirta* and *R. glabra* often occur as socies in this associes.

Secondary species: The most abundant secondary shrubs are *Rosa blanda, R. arkansana, Symphoricarpos occidentalis, Ribes gracile* and *Rhus rybergii.*

Herbs common to this associes will depend on many conditions, as the character of the surface soil, the plants present in the surrounding region, the time of clearing and the rapidity with which *Corylus* makes a covering. The following may be carried over from the climax association and persist under the *Corylus* if it is not too dry from the time of clearing until shade is reëstablished:

Actaea rubra	*Sanicula marilandica*
Aralia nudicaulis	*Smilacina stellata*
Erigeron philadelphicus	*Uvularia grandiflora*
Fragaria virginiana	*Vicia americana*
Lathyrus ochroleucus	*Viola papilionacea*
Lathyrus venosus	*Viola sororia*
Maianthemum canadense	*Washingtonia longistylis*
Polygonatum commutatum	

Those present as a result of invasion are *Aster laevis, Erigeron canadensis, Onagra biennis, Solidago canadensis, Zizia aurea,* and such grasses as *Elymus canadensis, E. virginicus, Agropyron caninum, A. tenerum* and *Agrostis alba.*

When the climax forest is removed and the land cultivated for a time and then abandoned, the shrub associes is slower in forming

than in the succession of uncultivated clearings. Furthermore it does not exist long before *Populus, Betula* and *Salix* seedlings enter, and the succession passes rapidly from the shrub associes to the *Populus-Betula* associes. The chief shrubs found in this associes are: *Rubus strigosus, Rhus glabra, Rhus rydbergii, Rosa blanda* and *Symphoricarpos occidentalis.* The herbs present are largely relicts of the preceding associes. After *Populus tremuloides* with its accompanying species has invaded, the succession of trees from then to the climax is essentially the same as described for uncultivated clearings on pages 359 to 361.

(3) *Populus-Betula* Associes

The presence of shrubs of the *Corylus-Rubus* associes by protecting the soil from exposure to the sun and wind maintains a higher water-content in the soil. The shrubs also afford protection to seedlings of *Populus* and *Betula* from excessive transpiration, thereby permitting them to become established.

Consocies: The consocies of this stage are *Populus tremuloides, P. grandidentata* and *Betula papyrifera. Populus* seedlings very soon appear after the establishment of *Corylus* and *Rubus* in the spaces not occupied by the latter. Their growth is slower than *Corylus,* and several years are sometimes required for *Populus* to rise above the tops of *Corylus. Populus* appears in practically all clearings. The occurrence of *Betula papyrifera* is somewhat irregular. In some localities it is absent, while in others it is sparse. In its range it is a very prominent consocies. Sometimes species of Salix, especially *S. discolor,* are numerous in the early stage of the *Populus-Betula* associes. The most important shrubs are as follows:

Amelanchier canadensis
Amelanchier spicata
Cornus paniculata
Prunus serotina
Prunus virginiana
Rhus hirta
Rosa blanda
Sambucus racemosa
Xanthoxylum americanum

Occasionally *Celastrus scandens, Parthenocissus occidentalis* and *Vitis vulpina* are found.

The herbs common to this associes are:

Actaea rubra	*Smilacina racemosa*
Anemone quinquefolia	*Smilacina stellata*
Aralia nudicaulis	*Thalictrum dioecum*
Aster drummondii	*Uvularia grandiflora*
Caulophyllum thalictroides	*Vicia americana*
Fragaria virginiana	*Viola papilionacea*
Hydrophyllum virginianum	*Viola pubescens*
Lathyrus ochroleucus	*Viola rugulosa*
Lathyrus venosus	*Viola sororia*
Sanguinaria canadensis	*Washingtonia longistylis*
Sanicula marilandica	

(4) *Acer-Tilia* Association

In the later stages of the *Populus-Betula* associes, *Acer saccharum, Fraxinus lanceolata, F. americana, Carya cordiformis, Ostrya virginica, Quercus coccinea, Q. macrocarpa, Q. rubra, Tilia americana, Ulmus americana* and *U. fulva* enter the associes and replace the existing dominants. This is merely a transitional stage between the associes and the final deciduous climax stage described under the *Acer-Tilia association* on page 367. In addition to the trees mentioned above, *Acer spicatum* in the northern and eastern edge of the deciduous climax association enters in the final stages of the *Populus-Betula* associes.

b. Secondary Succession in the Larix-Picea Subclimax

The discussion of secondary succession in the *Picea-Larix* subclimax as given for the same subclimax in the pine forest region on page 361, applies here with but few differences. Farther south, *Picea* disappears, so that the *Larix-Picea* associes is represented by *Larix* only.

The causes work in the same way and may operate singly or together, as indicated on pages 355 and 356. Fire, as the more destructive agent, affects the habitat more profoundly and causes succession to begin at a lower stage. This is especially true if burning occurs during a dry season when the *Sphagnum* surface is partly dry. At such times burning may result in killing out the *Sphagnum* and in the initiation of a secondary succession beginning with *Carex-Calamagrostis.* The sequence of stages after the appearance of *Carex-Calamagrostis* up to *Larix-Picea* is essentially that of primary succession as indicated on page 364.

When a tamarack swamp is drained and afterward burned, the succession begins usually with the *Carex-Calamagrostis* associes. As a result of the combined draining and burning, all the characteristic plants of the swamp disappear. The water-content of the habitat is still high but much less than if *Sphagnum* were present. The disappearance of *Sphagnum, Larix* and other swamp species permits the invasion of species of *Carex* and *Calamagrostis,* so that the *Larix-Picea* stage comes to be replaced by this associes as the first stage of secondary succession initiated by draining and burning. If the area affected be mowed or burned over each year, it may be kept indefinitely in this stage and valuable hay meadows result. If the swamp be kept drained but not mowed nor burned over, a secondary succession culminating in the climax *Acer-Tilia* forest will ultimately result.

In such a case the *Carex-Calamagrostis* associes is invaded first by *Betula pumila* and *Salix petiolaris* soon followed by *Salix bebbii, S. discolor* and *Cornus stolonifera.* In the region bordering on the climax pine forest, *Alnus incana* may also occur. As a result of the invasion of these, the plants of the *Carex-Calamagrostis* associes are killed out. The swamp gradually fills up by the washing in of soil around the edge, aided by the accumulation of humus from the decay of dead vegetation. The process of filling reduces the water-content of the soil and permits the invasion of *Populus* and *Betula,* and occasionally plants of *Fraxinus nigra* and *Abies balsamea.* Nearer the pine forest region, *Abies* is present more abundantly. The invasion proceeds from the edge, gradually encroaching on the swamp. After a time an associes of *Populus* and *Betula,* as described on page 373, becomes established. With the occurrence of a windthrow or by the death of individuals of *Populus* or *Betula,* the spaces left vacant are invaded by *Acer, Tilia* or *Ulmus* or by two or more of them together. The seedlings of these are able to grow in rather dense shade, and continue to develop until they finally overtop the poplars and birches, resulting in the death of the latter. In this way the climax *Acer-Tilia* forest, as described on page 367 under normal primary succession, becomes established. The successional stages of secondary succession in drained swamps from the initial stage up to the climax *Acer-Tilia* forest proceed more rapidly than in normal primary succession, but in stages common to both, the composition of the associes and the secondary species present are essentially alike.

The removal of the dominant *Larix* or *Larix-Picea* layer when not followed by burning, does not seriously affect the successional sequence since the water relations of the habitat remain essentially unchanged. The most marked effects are in the changed light relations and in increased exposure to evaporation. These changes may result in the disappearance of some of the shade-loving plants.

In extensive swamp areas where filling from the edge cannot alter the general conditions of the swamp, the effect of clearing is to permit the development of the bog shrubs which had been suppressed by the tamarack and spruce, and the consequent reëstablishment of an associes of *Andromeda* and *Chamaedaphne* when these are present. If *Andromeda* and *Chamaedaphne* be lacking, as happens in some areas, or present only in small numbers, an associes consisting of *Betula pumila* and species of *Salix* makes its appearance. Usually the clearing is not complete, a greater or lesser number of young tamaracks being left. These now develop and with their appearance the original dominant layer of *Larix* soon becomes established again.

In small, shallow swamps and in a zone along the edge of larger swamps where the soil is built up more as the result of filling in, an associes of *Cornus stolonifera* and species of *Salix* appears after the removal of *Larix* and *Picea*. Farther northward, *Alnus incana* appears as one of the consocies along with *Cornus* and *Salix*. *Betula pumila* often occurs with these also.

This *Cornus-Salix* zone is later invaded by *Populus* and *Betula papyrifera,* with occasional individuals of *Abies* and *Fraxinus nigra.* The invasion of these results later in the establishment of the *Populus-Betula* associes. With the occurrence of windthrows or the death of individuals in this associes, the spaces occupied by them are invaded by seedlings of *Acer, Tilia, Ulmus* and others of the climax forest, so that the climax comes to replace *Populus* and *Betula* as previously described.

The occurrence of windfalls are to be regarded as miniature clearings. In a *Larix-Picea* swamp in the deciduous forest area when a windfall occurs, its place is invaded at once by *Larix* and *Picea,* or by *Larix* alone toward the south, which results in keeping the area indefinitely in the same developmental stage. This applies in deep swamps where *Sphagnum* is abundantly developed.

In swamps that are more nearly filled up and where in conse-

quence, *Sphagnum* makes little or no growth, *Betula, Populus* and sometimes *Ulmus* appear in the places left vacant by windthrows. *Cornus stolonifera, Salix discolor* and farther northward, *Alnus incana,* often come in also, but these are later replaced by the trees named above. As the swamp fills up a *Populus-Betula* associes becomes established, to be succeeded finally by the climax *Acer-Tilia* forest, as the process of filling is carried still further.

A *Larix* or *Larix-Picea* swamp, if drained and not disturbed by clearing or burning, gradually fills up, thereby reducing the water-content of the soil. With the draining away of the water and filling up by washing in of soil along the edges, *Sphagnum* disappears. As the filling proceeds, *Larix* dies out, *Populus, Betula, Ulmus* and occasional individuals of *Abies* and *Fraxinus nigra* taking their places. In that part of the region bordering on the climax pine forest, *Picea, Abies, Betula* and *Fraxinus* are the usual dominants following *Larix* as the swamp becomes filled up. These, as filling proceeds, are replaced by *Acer, Tilia* and other trees of the climax forest. As the result of drainage not complicated by the introduction of other factors, the normal succession from the *Larix-Picea* associes to the climax *Acer-Tilia* forest takes place.

The results of the study of succession in Minnesota are essentially in accord with the findings of Cowles (1901), Whitford (1901), Transeau (1903), Coulter (1904), Howe (1910), and others who have made a study of swamps and climax forests in Michigan, Ohio, and eastward to Vermont.

Cooper (1910) has concluded that on Isle Royale the climax forest is an association of *Abies, Picea* and *Betula,* and he regards this as the climax vegetation of parts of northern Minnesota and north and east into Canada. As concerns Minnesota at least, this does not appear to be the case. The *Abies-Picea-Betula* stage is rather to be regarded as an associes which may in places persist indefinitely as a subclimax. It seems probable that such is the case on Isle Royale. Where these trees are dominant in Minnesota, the islands or parts of the mainland are low, and the water-content of the soil too high to permit the invasion and establishment of *Pinus.* With the building up of the soil or as a result of any other change which would decrease the water-content of the soil, *Abies, Picea* and *Betula* would undoubtedly be succeeded by the *Pinus* association.

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THE EFFECTS OF CERTAIN RUSTS UPON THE TRANSPIRATION OF THEIR HOSTS

J. E. Weaver

Transpiration has long been an interesting and important subject for investigation. But, notwithstanding the vast amount of research that has been done on the measurement of transpiration, at first independently of the relation to the physical environmental factors, and more recently with exact measurements and correlations of these, a survey of the published work discloses few studies upon the transpiration of diseased plants. The present paper reports the results of experiments with rust-infected and healthy plants of eight different species, of which the transpiration was measured for a total of more than 200 individuals. The period of investigation extended from October, 1914, until April of the following spring.

Review of Previous Investigations

Although it is frequently assumed that the presence of disease affects the rate of transpiration, there is very little published experimental data to support this assumption. Blodgett[1] has reported an instance of relative transpiration in a healthy excised branch of *Rubus sp.* as compared with a similar branch infected with *Gymnoconia interstitialis.* The branches were cut from adjacent plants (on May 24) and immediately placed in water. "The leaf surface was slightly greater in the healthy specimen, as the normal leaves were larger than the rusted, but the number was nearly equal in the two specimens. Large test-tubes were used, in which the branches were left tightly corked over night. When examined on the morning of the 25th the healthy branch was not wilted, the rusted one was considerably so. The rusted specimen evaporated 42 cc. while

the healthy specimen evaporated 23 cc. of water under parallel conditions.

"Thus the branch with the rusted leaves absorbed nearly twice as much water as the healthy branch, and yet failed to remain unwilted. The rust covered the lower surface of nearly all of the leaflets almost completely, and the extra demand for water thus imposed upon the plant was equivalent to doubling the leaf surface, as indicated by the volume of water transpired."

Dr. Harry B. Humphrey, Pathologist in Charge of Cereal Disease Investigations, of the Bureau of Plant Industry, has kindly furnished me with the data on an experiment which he performed in the physiological laboratory of the University of Minnesota in 1906. He compared the rate of transpiration of rusted and non-rusted wheat plants. He used two paraffined wire baskets, each containing four wheat plants. The baskets were effectually sealed so that water loss could take place from the plants only. After the first two leaves of each of the four plants in one container were badly rusted, as a result of an inoculation with uredospores of *Puccinia rubigo-vera*, the loss of weight from the two baskets was determined for a period of 22 hours, a part of which time the plants were in full sunshine out of doors. The loss in grams per unit area was calculated and it was found that the rust-infected plants transpired 38 per cent more water than the healthy plants of the same size and age. The area of the rust pustules was less than one per cent of the transpiring surface.

Reed and Cooley[6] have carried out a series of experiments upon the transpiration of apple leaves affected with the cedar rust fungus, *Gymnosporangium Juniperi-virginianae* Schw. The work was carried out on leaves and twigs on the trees in their normal position. Small branches of similar leaf area were enclosed in glass cylinders and the amount of transpired water was measured by the increase in weight of calcium chloride, which absorbed the exhaled moisture as it was continuously drawn from the glass cylinder through the calcium chloride tube. Fifty-two determinations were made upon healthy and diseased leaves of York Imperial and twenty-six upon the leaves of Ben Davis. Each experiment extended over a period of approximately two hours, and experiments were made at various periods of the day from July 9 to August 20, 1911, and July 26 to August 23, in 1912. They found that the unit transpiration of the diseased leaves of both varieties of apples was in the majority of

cases less than that of the healthy, and that the ratios were in general the same at any given period of the day. They determined the average ratio of transpiration for the diseased and healthy leaves of the York Imperial to be 78.3 and for Ben Davis 74.2.

An Analysis of the Project

Stated briefly, the aims of the present investigation were:

To determine whether or not rusts increase transpiration.

To determine the relation between the increased transpiration and the extent of the affected area.

To determine the time of the beginning, and the rate of the increase.

To determine the behavior of rusted plants and controls, as regards transpiration, under different environments.

To determine these relations for several species of plants, chiefly cereals, and for several kinds of rusts.

These determinations were made by means of the following plant materials:

Plant parts of same age, size, thickness, etc. (example, isolated opposite leaves).

Plants of approximately constant transpiring area, kept thus by clipping off new parts (example, wheat).

Entire plants: (a) experimented with for short periods so that increased growth would be small; (b) experimented with for longer periods where growth would be approximately proportional, or where the original and final transpiring areas were measured.

Since the purpose of the investigation was to determine the relation of water loss between diseased and healthy plants, extreme precautions were taken to keep all of the environmental factors exactly the same for both kinds of plants throughout an experiment. The method varied somewhat, depending upon the kind of plant used, but since most of the work was done with the smaller cereals, a typical case may be given, departures from which will be noted as other types of plants are discussed.

The plants were grown in ordinary glass tumblers of about 250 cc. capacity. An ordinary sandy-loam potting soil was used. To insure equal volume, water content, and aeration, the soil was screened through a 2-mm.-meshed sieve, brought to good tilth, and again screened through a 5-mm.-meshed sieve, after which it was

kept ready for use in a large covered earthenware jar. When filling the tumblers, they were constantly jarred in order to compact the soil, and enough soil was added to fill them to within 5 mm. of the top. The seeds of the cereals were germinated in a moist chamber and then planted in the soil contained in the glasses. About six seeds were planted in each container. These were then set away under bell jars in a warm place and in diffuse light until the plants were from 3 to 5 cm. high. Small dishes of water were placed with the plants under the bell jars.

Inoculations with the uredospores of the various rusts were made when the first leaves had reached a length of from 2 to 4 cm. This was accomplished by transferring the rust spores with a bent dissecting needle, from fresh stock material always kept on hand, onto the new leaves which had previously been wetted and rubbed lightly between the thumb and finger. After inoculation all the containers to be used in the experiment were placed in pans of water and again kept under the bell jars for a period of about 24 to 48 hours. Seventy degrees Fahrenheit was found to be the optimum temperature for infection.

By the end of the inoculation period the first leaves were mostly full-grown, and since determinations of relative transpiration were made before as well as after the appearance of the rust pustules, the glasses were at once sealed to prevent water loss from the container except that transpired by the plant.

Before sealing, the glasses were removed from the bell jars and the plants thinned down to 3 to 5 in each container. The less vigorous plants were always discarded. Then the soil was smoothed, the top of the glasses wiped clean and the wax seal applied. This consisted of a mixture of 80 per cent paraffin, with a melting point of 45° C., and 20 per cent petrolatum. The mixture was poured around the plants when it had cooled down to 48° C. This soon congealed and formed a seal covering the soil to a depth of 2 or 3 mm. and adhering perfectly to the glass and the plant stems without injuring the latter. However, considerable care in the application of the seal was necessary. It was found that plants just out of the inoculating chamber, if at a low temperature, were apt to be injured by contact with the warm wax. Also, under such conditions the wax adhered less perfectly to the glass. A warm knife-blade was sometimes used to remelt the edge of the wax seal and make the contact with the glass more certain, while invariably a large number of con-

tainers of both rust-infected and control plants were carried this far in the experiment so that enough would be left should an accident occur to any of them. In some cases where the first leaves were not fully grown, the plant was kept on the greenhouse bench over wet sand for a day or two, and then a few hours before sealing equal amounts of water (10 to 25 cc.) were added to each glass. Several trial tests showed that containers without plants but filled with soil and covered with the wax seal lost no measurable amount of water during a period of several weeks.

It is believed that by the use of these methods and by keeping the containers side by side throughout the experiment, the root environment, as regards kind of soil, its volume, water content, temperature and aeration, was made the same for all plants.

The method of measuring the amount of transpiration was by determining the loss of weight of the containers. The first weighing was made soon after the glasses were sealed. Weighings were made on a balance sensitive to 2 milligrams under the load thus imposed upon it, about 500 grams. The second weighing was usually made about 24 hours later, care being taken to keep the plants in a fairly humid atmosphere during this first interval, so that they would not be injured by a too sudden change from the moist air of the bell jars. Further weighings were taken, usually, at intervals of about 48 hours, until the plants, which were growing in the greenhouse, showed indications of the leaf tips drying up.

In order to keep the transpiring area approximately constant, only the first leaf was allowed to grow. The second leaf of each plant was clipped daily. At no time was the humidity so high as to produce guttation, and although the growth of the second leaf was about 1 cm. each 24 hours, this was entirely comparable in all the plants and the error of varying area thus introduced is believed automatically to have checked itself out.

Usually four containers of infected plants and four of control plants constituted a battery for a single transpiration determination, although the number was sometimes less. All of the plants in a battery were kept under exactly the same conditions throughout the experiment. A constant record was kept of the light condition (sunshine or cloudiness), temperature, humidity, and the evaporating power of the air. A few of the later experiments were carried on in a large glass case of about 1.3 cu. m. capacity, and here the factors of humidity and temperature could be kept under better con-

trol (Plate XLI). However, since all the plants in any determination were under similar conditions, the reader need not be burdened with these data of factor measurements, and they will be omitted except where they help to explain certain interesting results.

The determination of the transpiring area was made as soon as any of the leaves, which often kept an upright position throughout the experiment, showed signs of drying at the tip. This occurred from 8 to 14 days after the plants were sealed. It may be stated here that this is a normal process and was not due to lack of moisture, for at the end of the experiments the soil was usually still in good tilth condition. At the conclusion of an experiment the plants were placed in a very humid atmosphere until they were turgid, then the leaves were clipped at the ligules and those of each container placed together. Photographic prints of the leaves were then made, using solio printing paper. The white portions representing the leaves of each group were cut out and weighed on a balance sensitive to 0.5 milligrams. Knowing the weight of one square decimeter of the solio paper, the area of the solio leaves was easily calculated. The area thus obtained is, of course, that of one side of the leaves only and must be doubled for the total leaf area. To get the total transpiring area it was necessary to add to the leaf areas thus determined the area of the culms. These were cut off at the surface of the wax seal. The area was determined by multiplying the culm length of each plant by its average diameter by 3.1416. Four diameter readings were made for each culm by placing it on a millimeter ruler under a reading glass.

Finally, the loss of weight in grams of each container for each period was divided by the total transpiring area of the plants it contained expressed in square decimeters. The quotient was the transpiration in grams per square decimeter for the period under consideration.

A slight source of error in this method might arise from the fact that final transpiring surfaces were used to calculate earlier water losses. However, it has been pointed out that the first leaves were apparently full-grown at the beginning of the transpiration measurements and any increase in growth would probably be proportional in all the plants used.

Several weighings were made to determine the uniformity in weight of the solio paper. The readings are shown in the following table.

	No.	Grams
Solio per sq. dm.	I	1.860
" " " "	II	1.861
" " " "	III	1.857
" " " "	IV	1.839
" " " "	V	1.841
" " " "	VI	1.849

Average weight of 1 sq. dm., 1.851; greatest variation from the average, 0.012; greatest variation from the average in per cent of average, 0.6 per cent.

From these figures and other similar ones it appears that the solio paper was unform within one per cent of error.

Finally, it may be stated that the shrinkage of a turgid leaf placed between the solio paper and the glass of the printing frame is practically nil during the short period necessary to get a leaf print of sufficient clearness to be plainly seen.

The method for accurately determining the area of the rust pustules was not so easily found. Finally, the following plan was used. It combines ease of manipulation with a high degree of accuracy. The parts of the leaves which bore pustules were cut off, and solio leaf prints made as above described. The leaves were then again placed in a moist chamber and the surface spores removed by means of a camel's hair brush. Then they were quickly placed in a row on a clean smooth piece of glass and at once covered with a similar piece, the two fitting closely together. This held them flat and at the same time allowed little water loss. They were then photographed, first the lower surface and then the upper. The latter was accomplished by simply turning the glass plates over, and without readjusting the camera (Plate XLII). The longest leaf photographed was measured, and from the prints an enlargement of ten times the original size was made. This increased the size of the pustules to dimensions that could easily be worked with (Plate XLI). Each leaf of the enlargement was carefully compared with the original leaf and any spots or dots (of which there were few) not corresponding to a rust pustule, were eliminated. After weighing the enlarged leaf prints (the upper and lower surfaces of which fit exactly back-to-back) the pustular area of each was cut out and weighed. From this data the per cent of rusted area could easily be calculated. By weighing the solio prints of the parts photographed and determining their proportional relation to the total transpiring surface, it was possible to determine the per cent of the pustular area based on the total transpiring surface.

The variation in weight of the enlarging paper was found to be not greater than 5 per cent. This error, however, automatically reduced itself to a negligible quantity when the pustular area based on the entire transpiring surface was determined.

While the whitish areas which develop about the pustules may increase transpiration, Stakman[10] has shown that at least for a long time in non-rust-resistant varieties (such as those used in these experiments) the cells remain intact, and although the normal stomatal activity may be affected, it is certain that the epidermis is not ruptured except at the pustules. When physiologists have devised a method of measuring the real internal transpiring surface of a leaf, we may be able more nearly to calculate the affected transpiring area of rusted plants.

Experiments with Wheat

The wheat used in these experiments was a bluestem, Minnesota No. 169, which was obtained from Mr. John Parker of the Bureau of Plant Industry, who was then stationed at the Minnesota Agricultural Experiment Station. He also furnished the seed of the other cereals used. This wheat was inoculated with uredospores of *Puccinia graminis tritici*. This rust, as well as the others used on the small grains, was obtained from the stock cultures of Dr. E. C. Stakman at the University Agricultural Experiment Station, and afterwards kept growing on stock materials in the greenhouse physiological laboratory of the University of Minnesota, where the experiments were performed.

The first weighings were made at 3 p.m., January 29, and following weighings on alternate days until 10 a.m., February 12, when the experiment was concluded. The results have been plotted in the form of graphs in figure 1. The light solid line gives the transpiration in grams per sq. dm., as indicated on the y axis. It represents the water loss of six healthy plants in two containers. The abscissae represent the intervals of time between weighings. Similarly, the heavy solid line gives the same data for seven rusted plants in three containers. The broken line shows the evaporating power of the air as determined by Livingston's standardized porous cup atmometers, which were operated near the plants. These data have been reduced to that of the standard atmometer.[3]

A glance at the graphs shows that at the beginning the transpiration of the rusted plants is somewhat higher than the controls.

This, as further data will show, is merely a variation of the individuals, and is not due to rust infection. On February 3, tiny whitish areas began to appear and by the 5th numerous rust pustules had broken through the epidermis. From this time there may be

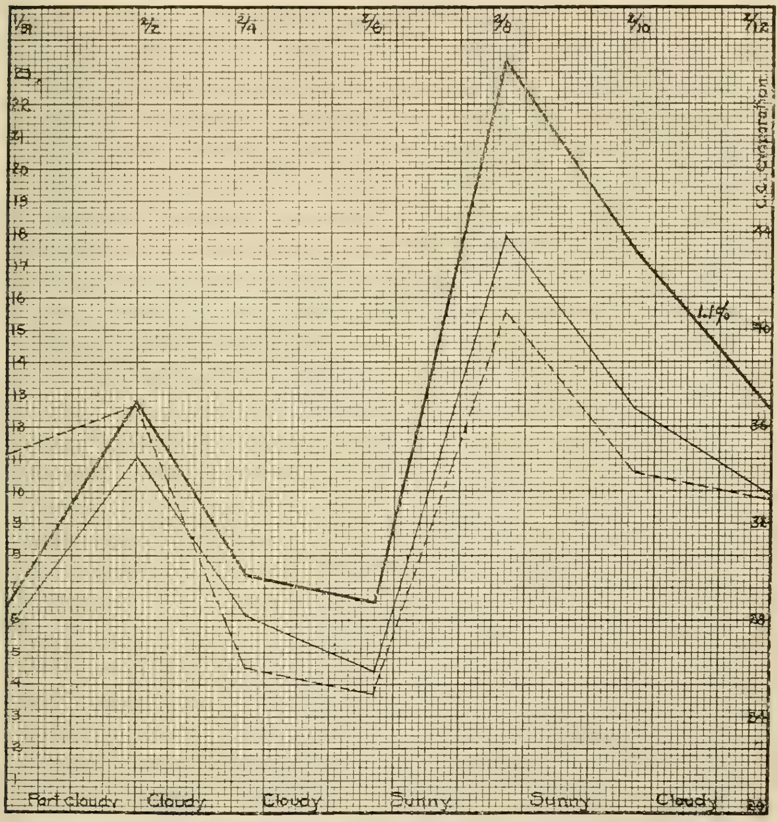

Fig. 1. Graphs showing the relative transpiration of healthy and rust-infected wheat plant. The broken line gives the evaporation in cc. during the same intervals, as measured by porous cup atmometers.

noted a decided increase in the water loss of the rusted over the healthy plants. The final rusted area for the seven plants averaged only 1.1 per cent of their transpiring surface.

The close similarity in the general course of the graphs is no less striking than their greater divergence when more severe environmental conditions were brought to bear upon the plants. While the graph of evaporation gives a rather satisfactory summation of

these conditions,[4] a still closer analysis of this particular case may be given as it will help to explain similar conditions in the future.

The first period of increased transpiration was due to partly sunny weather. This was followed by four days of cloudiness. During this second period the hydro-thermograph registered a mean

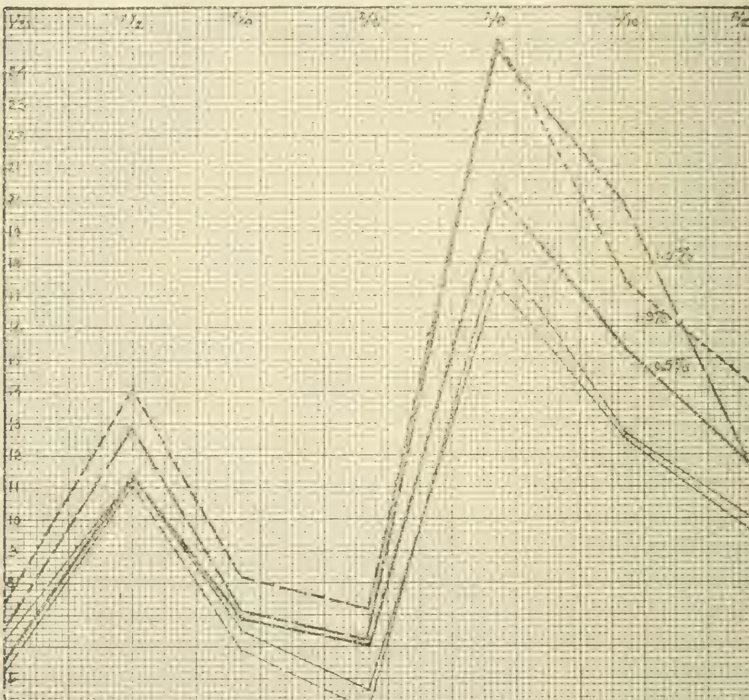

Fig. 2. An analysis of the combined graphs shown in figure 5. The light lines indicate transpiration rates of control plants.

of 70° F. with a range of about 10° F. while the relative humidity fluctuated only a little above or below 50 per cent. Then came a period of four days of sunshine when the day temperatures mounted to 80° to 85° F. and the humidity at the same time decreased. Finally ensued a period of cloudiness when again both evaporation and transpiration were lessened.

In figure 2 an analysis of the combined results shown in figure 1 is given. Here the variations of the plant groups of the different containers may be seen. It may be noted that the rusted plants giving the greatest variation from the controls at the beginning, likewise give the greatest variation in general throughout. The per cent of pustular area of each plant group is designated on the chart.

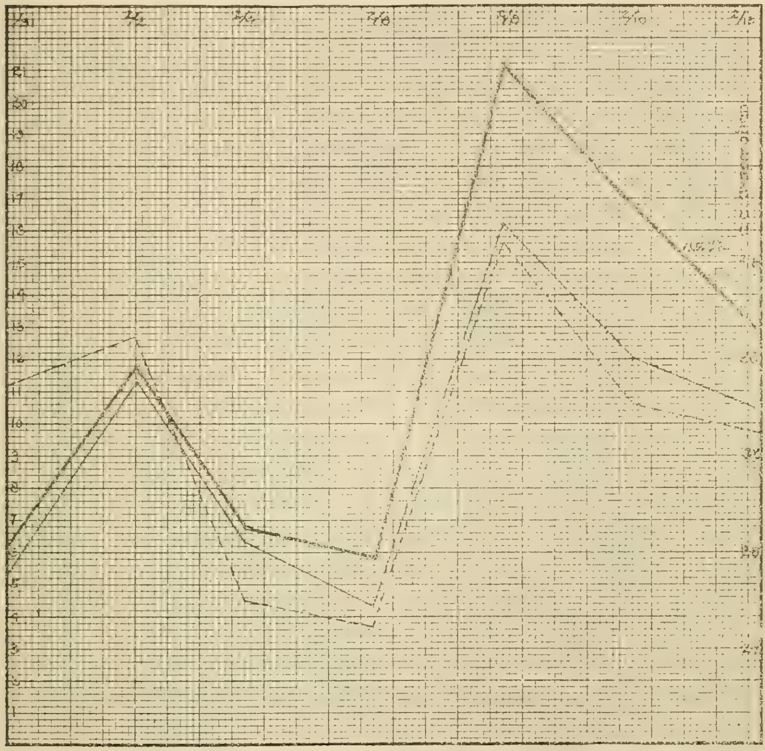

Fig. 3. Graphs showing the relative transpiration between 12 healthy and 16 rusted wheat plants. The broken line is the evaporation graph.

A relationship may be seen between the amount of rust and the transpiration rate, although this is more clearly shown in other cases.

A second battery of wheat consisting of nine similarly rusted plants in three containers, and six healthy plants in two containers was carried on at the same time as the preceding and under exactly the same conditions. Since average results from a large number of

plants more nearly show actual conditions, by smoothing over any individual variations which are certain to occur in all biological experiments, these data are combined with those of the preceding and shown in figure 3. Here the solid line gives the transpiration of twelve healthy plants and the broken line that of 16 rusted plants

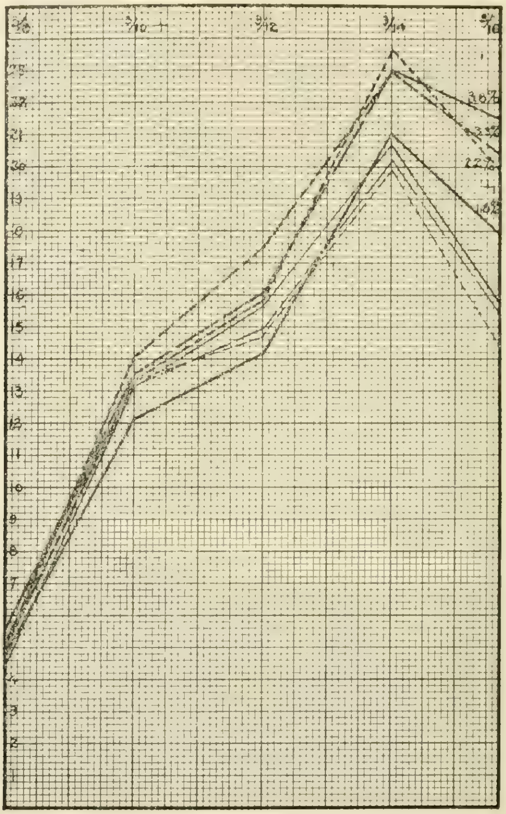

Fig. 4. Graphs showing relative transpiration rates between 11 control and 14 diseased wheat plants.

with an average pustular area 0.9 per cent of the transpiring surface. It may be mentioned that an analysis of the second battery here included gave results very similar to those shown in figure 2, but with a closer agreement between the graphs representing the transpiration of the diseased plants.

On March 7 the first weighing was made on another battery of

wheat plants consisting of eleven control and 14 diseased plants infected with *Puccinia graminis tritici.* The experiment was continued until March 16, a period of nine days. The results are shown graphically in figure 4. Here again the heavy lines represent the diseased plants and the light lines the controls. The apparent low loss of water of these plants during the first period is due in part to the shorter interval between weighings (here 24 hours) and in

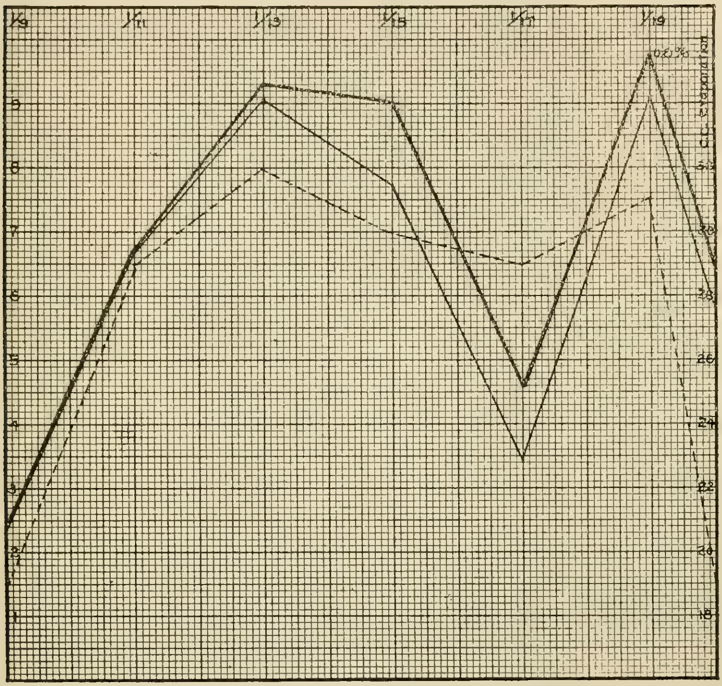

Fig. 5. Graphs showing the relative transpiration of healthy and rust-infected rye. The broken line shows the evaporating power of the air as measured by porous cup atmometers.

part to the fact that after removing the plants from the moist atmosphere of the inoculating chamber it was expedient to keep them in a fairly humid place for a time.

The pustules began to appear on March 11 and by the 13th were quite abundant, except on the plants indicated by the lowest heavy line, where for some reason their appearance was delayed until about the 13th.

A striking relationship between increased transpiration and

amount of rust is here evident, and this, with one exception, was found in all cases. The difference was often evident when an increase of only a fraction of one per cent was involved.

A fourth battery of wheat plants, consisting of 12 controls and eight rust-infected plants, was run from January 8 to January 20.

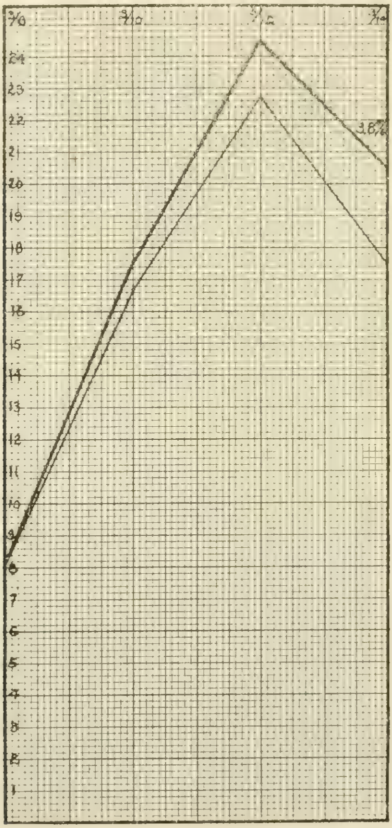

Fig. 6. Graph showing the relative water loss from 12 control and 9 diseased rye plants.

The results were so similar to those of the cases already given that they need not be recorded here.

Experiments with Rye

On January 8 a battery consisting of eight control plants and three infected plants of spring rye, the latter inoculated with *Puc-*

cinia rubigo-vera secalis, were weighed for the first time. The successive transpiration losses are shown in figure 5. The dates on the abscissae indicate the length of the intervals between weighings. Throughout the period the sky was clouded much of the time and conditions for maximum transpiration, as indicated by the evaporation graph, were poor. Notwithstanding the fact that the rusted area was small (only 0.8 per cent), still the appearance of the pustules on January 13 and 14 was accompanied by a marked rise in the transpiration of the rusted plants over the controls.

From March 7 to March 14 relative transpiration data were obtained from a battery of 9 rusted and 12 control rye plants. The

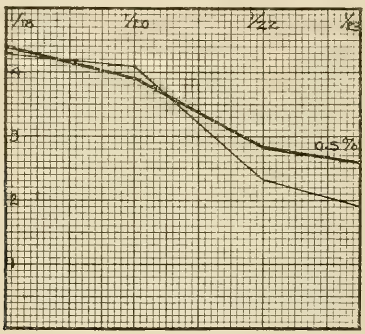

Fig. 7. Graphs showing the relative transpiration of healthy and rust-infected oat plants.

same rust was used as in the preceding case. The results are shown in figure 6. The first rust pustules began to appear on March 9 and 10, and by the 14th a total pustular area of 3.8 per cent was determined. During the last two days of the experiment, the plants, because of high temperatures (85° to 92° F.) and low humidities (20 to 30 per cent), were kept in a semi-wilted condition. However, no differences in the degree of wilting between rusted and control plants could be determined. An analysis of the combined graphs into their component parts shows that the plants with 6.5 per cent of rusted area transpired during the last 4 days 8 grams more per square decimeter than plants with only 0.9 per cent of infected area. The graph for the plants with 4 per cent of rust showed transpiration rates intermediate between these extremes.

A third experiment with rye was conducted from November 15

to November 23. Here again the results in all cases gave a higher transpiration rate for diseased plants. Since they merely confirm the evidence already given they need not be included.

Experiments with Oats

An experiment with White Russian oats, rusted with *Puccinia graminis avenae,* was carried out from January 16 to the 23rd. Eight diseased and nine control plants, making a battery of eight containers, were used. During nearly the entire period conditions for transpiration were unfavorable. The results are shown in figure 7. The rust pustules began to appear on January 20 and were well out by the 22nd. The rusted area was not measured as in the foregoing experiments, but a careful count of the number and measurements of the average size of rust pustules gave a total pustular area of 0.5 per cent. It may be noted that while the relative transpiration was low, the increase of the rusted over the healthy plants was, during the last interval, 37 per cent.

Earlier experiments with oats were conducted for shorter intervals of time and just after the rust pustules had appeared. A part of these data are recorded in table I. In these experiments the amount of rust ranged from a light to a very heavy infection, but the exact amount was not determined.

TABLE I

Date of the beginning of experiment	Duration in hours	Condition of plant	Transpiration in grams per sq. dm. of transpiring surface	Percentage of water transpired
Nov. 22	70.5	healthy	9.252	100
		healthy	10.060	
		rusted over entire leaf area	45.174	467
Nov. 26	153	rusted	20.502	212
		healthy	23.599	100
		healthy	27.706	
		rusted*	49.908	194
Dec. 14	121	healthy	14.347	100
		healthy	11.301	
		rusted	15.604	121
		rusted	17.395	135

*In this experiment the rust used was *Puccinia coronata.*

From these data it is evident that these rusts on oats not only increased transpiration in all cases but that in some instances the increase amounted to several times that of the normal water loss.

Experiments with Barley

The following experiments, which are illustrative of others conducted with Odessa barley rusted with *Puccinia graminis hordei,* may be summarized in the table II. The rusted area was not determined.

TABLE II

Date of the beginning of experiment	Duration in hours	Condition of plant	Transpiration in grams per sq. dm. of transpiring surface	Percentage of water transpired
Nov. 28	91	Healthy	7.691	100
		"	7.408	
		Rusted	7.950	105
		"	8.515	112
Dec. 2	51	Healthy	5.704	100
		"	4.670	
		Rusted	6.336	122
		"	5.992	115
Dec. 15	67	Healthy	5.714	100
		"	6.362	
		Rusted	9.383	155
Dec. 22	164	Healthy	22.349	100
		Rusted	26.802	119

Experiments with Corn

In this series a yellow dent corn, Minnesota 13, was used. Uredospores of *Puccinia Sorghi* Schw. were collected from a field in October and the rust was kept growing on stock cultures in the plant house. The experiments with corn were performed before a satisfactory method for determining the pustular area had been devised. An approximation of the rusted area was made by cutting out and weighing the affected parts and comparing this with the total leaf weight. Further studies showed that this gave results quite too high. In these experiments with corn a single plant was grown in a container. In the experiments recorded in table III, plants were inoculated on the first and second leaves as soon as the

second leaves were about half unfolded, and no part of the plant was removed. The transpiring area was based on the final leaf area. Weighings were made soon after the pustules appeared. As far as observation can permit one to judge, the growth of control and rusted plants was proportional.

Since higher transpiration rates in diseased plants were invariably obtained, the results of only two experiments will be given in table III.

TABLE III

Date of the beginning of experiment	Duration in hours	Condition of plant	Transpiration in grams per sq. dm. of transpiring surface	Percentage of water transpired
Nov. 20	425	Healthy	4.896	
		"	5.240	100
		"	4.619	
		"	4.875	
		Rusted	6.021	122
		"	6.719	136
		"	5.169	105
		"	8.837	180
Nov. 21	114.5	Healthy	8.532	
		"	8.524	100
		"	8.002	
		"	8.240	
		Rusted	12.676	152
		"	8.767	105
		"	12.465	149
		"	11.043	132

The marked increased water loss as well as its constancy in all determinations leaves no doubt that here again rusts do accelerate transpiration.

Further experiments of a similar nature merely confirm those already given, so that only a single additional case with corn will be recorded.

On December 9 the first, second and third leaves of three corn plants were inoculated as usual and placed with four control plants in vessels of water under the bell jars. Two days later the glasses were sealed and weighed and weighings were made each day thereafter at nine o'clock in the morning, for 13 days. The results are shown in figure 8.

Whitish spots became visible on the 16th and by the 17th the pustules were breaking out. At the conclusion of the experiment the first leaves of some of both the healthy and rusted plants began to show signs of drying at the tips. Unfortunately, cloudy, humid weather kept down transpiration rates. Nevertheless the appear-

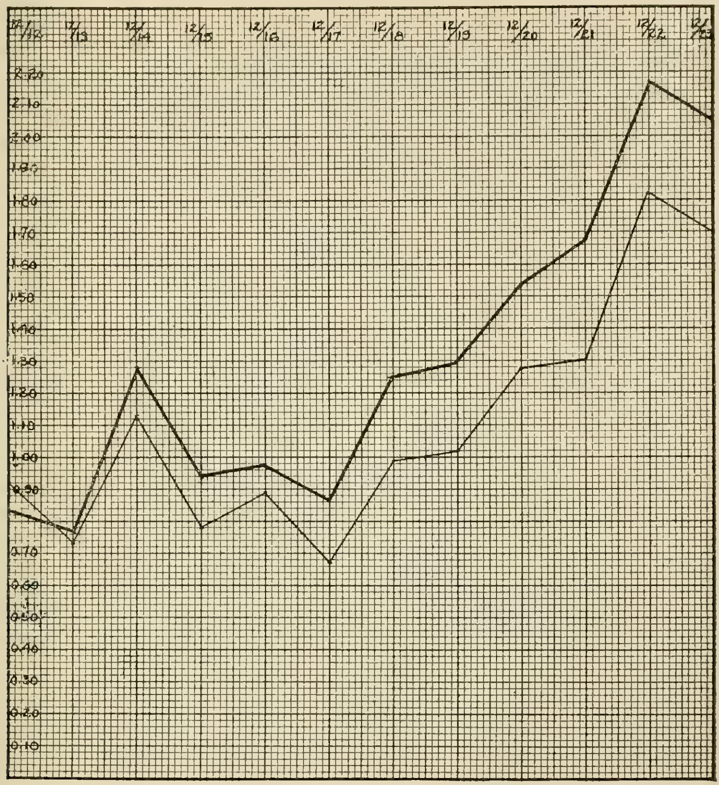

Fig. 8. Graphs showing the relative transpiration rates of 4 control (light line) and 3 rusted corn plants.

ance of the rust pustules is at once shown by the increased transpiration of the diseased plants over the healthy ones.

Dicotyledons

A series of experiments was performed to determine the relation of rusts to transpiration among certain dicotyledons. In fact the writer had hoped to include a number of species in this list, but

the press of other duties was such that the work here was limited to a few determinations on cockleburs, sunflowers, and carnations. The methods used are in general those already described, and the differences only need be pointed out.

Experiments with Cockleburs

Fruits of *Xanthium commune* Britton were collected from a nearby field on February 20, submerged in water for 24 hours, and planted in a sandy-loam soil in a flat on February 22. This was kept in a warm place in the greenhouse and when the cotyledons were just out of the soil, on February 27, the plants were potted, one in each glass, in soil prepared in the usual manner. Forty-five cc. of water was added to each glass at this time and the plants were placed under bell jars. Six days later the first pair of leaves was inoculated with teleutospores of *Puccinia xanthii* Schw., secured the previous autumn from cockleburs of the same species by Mr. Walter Muenscher at Lincoln, Nebraska. After inoculation all the plants were placed in pans of water under the bell jars for 36 hours, after which they were kept in a moist place until February 9. The glasses were then sealed, the cotyledons cut off, and the stems also cut just above the first pair of leaves. Then, by removing one end from a small printing frame and cutting a notch to admit the petiole, leaf prints were made and the leaf area was determined in the usual manner. This was done in the morning, and in the afternoon of the same day the first weighings were made. The plants were about 10 to 12 cm. high and the leaves about 2.5 cm. wide and 5 cm. long, exclusive of the petioles. At this time no external evidence of rust was apparent, nor had the conditions changed at the time of the second weighing 22 hours later. But soon after, yellowish patches began to appear which gradually increased in size and number. Simultaneously with their appearance a falling off in transpiration was noted. These data are shown in figure 9. Here may be seen a great decrease in the transpiration of the diseased plants. The difference in the rate of transpiration of the different diseased plants may be readily accounted for by the difference in the amount of infection. On March 15, the pustules were breaking out in various places but were not yet abundant. The experiment was discontinued because the tips of the leaves on two of the rusted plants showed signs of drying up. The rusted leaves were variously distorted.

Some stood at right angles to the normal position, some had turned in such a manner as to expose the under surface directly upwards, while all were more or less curled and twisted.

The final leaf area was measured, and in determining the transpiration loss interpolations were made so as to give the leaf area during the intervening periods. The increase in leaf area was

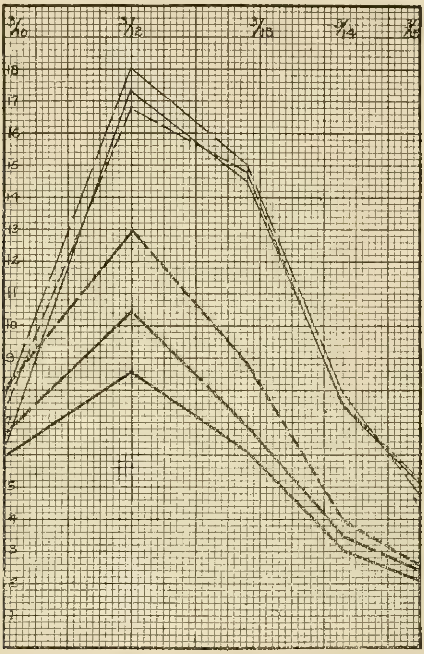

Fig. 9. Graphs showing relative transpiration rates between healthy and rusted cockleburs. The heavy lines show the transpiration of diseased plants.

nearly twice as great in the healthy plants, owing in part to the more vigorous growth of new leaves in the axils of both the cotyledons and the first pair of leaves. The diseased and control plants were found to have so nearly the same stem area, that it was not included in the transpiring surface, since the epidermis is all but destitute of stomata.

In order to check the preceding experiment, another series of healthy and infected plants was used. In this case the cotyledons only were removed and the first three or four leaves infected. The

results are strikingly similar to those above recorded and need not be given.

Experiments with Sunflowers

While the following experiments are only of a preliminary nature, still they throw light upon the rust-transpiration problem and may be briefly noted.

Three sunflowers of the same age, height, and approximately similar leaf area were selected from stock material in 4-inch pots filled with ordinary potting soil. One of these plants was inoculated on November 14 with the teleutospores of *Puccinia Helianthi* Schw. found on a wild sunflower, probably *Helianthus annus.*

On November 29 and when only two rust areas had appeared, the plants were well watered and then placed in Ganong's aluminum shells. These were covered with sheet rubber and the wax seal in such a manner as to prevent loss of water except by transpiration. They were then weighed on a new "Cenco" trip balance sensitive to 0.1 g. and the transpiration losses determined for five intervals during the following 16 days.

From time to time during the experiment the plants were taken from the aluminum shells for aeration, and at these times the water lost by transpiration was replaced. At the end of the experiment when the transpiring area (exclusive of the stems) was calculated, the plants were 27 to 30 cm. tall, and they had from eight to ten leaves each. The diseased plant had rust on the five lower leaves. By cutting out the pustular areas and dividing the weight of these by that of the total leaf weight, the rusted area was approximated to be 17 per cent.

The results showed that during the first interval of the experiment the diseased plant lost 63 per cent more water than the healthy plants. This excess transpiration over the normal gradually diminished however, to 44, 36, 22, and 29 per cent respectively, at the successive intervals between determinations.

A second experiment was started on November 17, and when the rusted areas of a similarly diseased sunflower were just beginning to appear. The experiment was carried on for a period of eight days and exactly like the preceding, only 3-inch pots were used. The rusted area was about 15 per cent.

Here again, the diseased plant showed at first a decidedly in-

creased transpiration rate over the normal. This became progressively less and less, and during the last interval the rusted plant transpired 27 per cent less water than the control.

While the results are not conclusive, they are at least suggestive. Sampson and Allen[9] have shown that "variation in transpiration per unit area for a given time is found to be but slight for plants of the same species, when about the same age, grown and tested under similar conditions, whether in their natural habitats or in the plant house." Therefore an explanation of this phenomenon must be sought elsewhere than in the individual variation in the transpiration rates of the plants.

Experiments with Carnations

A non-glaucous variety of *Dianthus caryophyllus* L. was used in the following experiments. They were selected from stock material on hand in the greenhouse. The plants were about 9 cm. high, of approximately the same age and size. They were grown in 3-inch pots. On October 24 several leaves on one of these plants were inoculated with spores of *Uromyces caryophyllinus* (Schrank) Wint. After being two days in a saturated atmosphere under a bell jar the plants were then sprinkled thoroughly morning and night. The pustules began to appear in just 30 days. On November 28, when 15 patches of pustules had appeared, transpiration losses from the diseased plant and also from a healthy one similarly treated, were recorded. The methods were the same as those described for sunflowers. The experiment was continued until December 23, during which time six transpiration losses were determined. Throughout the experiment the plants showed about the same amount of growth. The final rusted area was approximated at 3 per cent of the total transpiring surface. During the whole period of 25 days the rust-infected plant lost slightly less water than the control. Unfortunately, no time was found to repeat the experiment. However, two experiments were performed with the excised leaves of carnation.

In these experiments leaves from three carnation plants similar to those previously used were employed. Rusted leaves were selected which had healthy leaves opposite them. These pairs were cut off under water as near the stem as possible and the ends placed through slits in corks sunk in the necks of small vials which were filled with water. The leaf surfaces were then dried as were also

the corks and necks of the vials. The vials were then sealed with the wax seal. Care was taken to assure a perfectly tight seal. The vials and contents were weighed, placed under good transpiring conditions for 48 hours and again weighed, the loss in weight being that of the water transpired. The leaves were then cut at the surface of the wax. Leaf prints were made in the usual manner and the lower surface of the leaves (the upper was without pustules) photographed and enlarged, and the pustular area calculated as usual. The results are shown in table IV.

TABLE IV

EXPERIMENT I

Leaf	Area in sq. cm.	Percentage of pustular area	Transpiration in grams per sq. cm.	Percentage of water transpired
1	.542	0	.1439	100
2	.620	5.1	.2161	150
3	.261	0	.0944	100
4	1.757	6.7	.1642	174
5	2.067	0	.1253	100
6	1.757	2.6	.1291	103
7	2.791	0	.0958	100
8	2.145	1.0	.1505	157

EXPERIMENT II

Leaf	Area in sq. cm.	Percentage of pustular area	Transpiration in grams per sq. cm.	Percentage of water transpired
9	1.059	0	.1435	100
10	.465	35.6	.2430	169
11	2.041	0	.0764	100
12	2.610	2.7	.0848	110
13	1.602	0	.1803	100
14	1.989	4.1	.1256	69
15	2.429	0	.0703	100
16	1.237	14.2	.1107	157
17	.491	0	.1873	100
18	.465	12.3	.1709	91
19	.439	0	.1913	100
20	.413	10.4	.2397	125

The marked differences in the transpiration per unit area of the control leaves may be due in a great measure to their differences in age and relative cutinization. There seems to be little correlation between the amount of the rusted area and the increase or decrease of transpiration. In most cases, however, a marked increase in the transpiration rate may be seen. Notwithstanding the results of the

preceding experiment (where only a small amount of rusted area was involved) and the two exceptions to the general results shown in the table, the writer is of the opinion that further experiments will reveal a higher water loss from rusted than from healthy carnations where they are grown under similar conditions.

Discussion and Conclusions

A review of the preceding data shows that without exception, the presence of the cereal rusts even in very small amounts has a decidedly accelerating influence upon the rate of transpiration. The increase in transpiration occurs about the time the pustules break through the epidermis and evidently continues for a long period of time. Further, a quantitative relation exists between the extent of the pustular area and the increase in the transpiration rate. This was evident, with one exception, in every case where the area of the pustules was measured, and indeed the relationship was so close that an increase of 0.2 to 0.3 per cent in the pustular area was registered by a definite increase in the transpiration rate. After most of the pustules were well broken out, any increase or dcrease in the accelerated transpiration rate was not apparent. It is possible that the older pustules permitted less water to escape while the initial accelerated transpiration rate was maintained by the appearance of new pustules. In most cases when more severe environmental conditions as regards transpiration were brought to bear upon a battery of cereals, the rusted plants gave a correspondingly greater rate of transpiration over the normal than before or after such a period of stress.

Although a close relation exists between the amount of excess water loss and the extent of the pustular area, still the writer does not hold that the cause of accelerated transpiration is due wholly to the torn epidermis. As is well known, whitish areas occur about the rust pustules. Even if the mesophyll cells in these regions do remain alive for a long time in susceptible hosts, as shown by Stakman[10] in the case of certain cereals, and by Ward[11] in *Bromus* sp., still their transpiration rate might be greatly altered. When these leaf cells become half filled with haustoria, as is frequently the case at the time of pustule formation, it is hard to conceive how they would function normally.

The increase in transpiration rate reported by Blodgett[1] for

Rubus sp. might be accounted for by the rupture of more or less extensive areas of the lower epidermis of the leaf due to the "Caeoma" type of sorus produced by *Gymnoconia interstitialis*. This would obviously accelerate transpiration from the underlying mesophyllic cells. But here also possibly other factors connected with the diseased condition may operate to cause increased transpiration. Perhaps deleterious substances are thrown off by fungi which materially alter the transpiration rate.

Reed[7] has shown that small amounts of tannic acid and pyrogallol accelerate transpiration. He also pointed out that substances like oxalic and acetic acid, which are found as such in plants, when in small amounts increased transpiration. Similarly Burgerstein,[2] working with solutions of camphor, found that solutions containing one part of camphor per thousand had an accelerating effect upon the transpiration of most plants investigated. Excised shoots which were previously allowed to become wilted revived more quickly when placed in camphor water than when placed in distilled water. By weighing the vessels of water in the two cases it was shown that transpiration from the shoots went on more rapidly in camphor water than in distilled water. That camphor was absorbed by the excised shoots was shown by their pathological condition and death prior to the appearance of any such conditions in the parallel series in distilled water.

This may properly be regarded as an example of transpiration under pathological conditions and it may be that deleterious substances thrown off by fungi act similarly to the camphor. However, only after careful biochemical investigations concerning the activities of invading hyphae and invaded host tissue are made can this question be definitely settled.

Whether due solely to the ruptured epidermis or in part to other causes acting in conjunction with this, it is certain that rusts increase transpiration to a marked degree even when infection is light, while a moderate infection may more than double the normal rate. Livingston[5] has shown that for wheat grown under ordinary transpiring conditions, the amount of transpiration is a rather reliable index of growth, when the latter is measured by the increase in green weight of the above-ground parts. However, it seems clear that the transpiration rate might under diseased conditions of the plant become so excessive as to be highly detrimental to it in carrying on its normal activities.

Just as the experiments with the cereals were characterized by a definite increase in transpiration of rust-infected plants, likewise rusted cockleburs showed just as positive a falling off of water loss. As already mentioned, Reed and Cooley[6] obtained similar results with rusted apple leaves. They pointed out that the fungus may work in one or more ways to diminish transpiration—either by its intoxicating action upon the host cells, or by causing hypertrophy, which alters the normal activities of the leaves. It would seem that the latter cause alone might be quite sufficient. The parts of the apple leaves bearing the clustercups are three or four times the normal thickness. The hypertrophy, as Reynolds[8] has pointed out, is due to an enlargement of the sponge cells to twice or thrice their normal diameter and the filling in of the intercellular spaces with masses of mycelium. The stomata are scarce or lacking and the sub-stomatal cavities are altogether lacking. Reed and Cooley concluded "that the hypertrophy of the leaf and the subsequent obliteration of intercellular space diminishes the possibility of water elimination from the interior of the leaf. The thick cushions on which the aecidia are produced have stimulated the leaf cells in that place to enlarge, and obliterate the stomata."

In the case of the rusted cockleburs changes even more profound than those above noted occur. The normal leaf tissue is very loosely formed. Very large air chambers permeate the spongy parenchyma and the palisade is scattered. Reynolds working with *Xanthium canadense* Mill. (?), parasitized by *Puccinia Xanthii* Schw. gives the following description:

"This [normal leaf] tissue . . . is in many places almost completely replaced by the fungous mycelium. The cells which remain have no protoplasm and are filled with oil globules. On both the upper and the lower leaf surfaces the mycelium is abundant and the telial spores are very numerous. Within the mixture of parenchyma cells and mycelium, which replaces the normal tissue, there are cystlike bodies which are composed of masses of mycelium. These objects are hollow spheres, and from the inner surface arise telial spores exactly similar to those borne in the normal way upon the exterior of the leaf."

The results with sunflower and carnation are by no means conclusive. It is apparent however, that the yellowish cushions upon which the pycnidia of *Puccinia Helianthi* are produced, are caused by hypertrophy of the underlying leaf tissue. No such change of

leaf tissue is evident in carnation. However, further experimental data on the relative rate of water loss as well as a study of the cyto-morphology of the diseased leaves is necessary before conclusions can be drawn.

The writer is indebted to Dr. F. E. Clements and Dr. E. M. Freeman for suggestions and efficient criticism throughout the course of the work.

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Figure. 1. Batteries of wheat, rye, and cockleburs used in determining the relative transpiration of healthy and rust-infected plants.

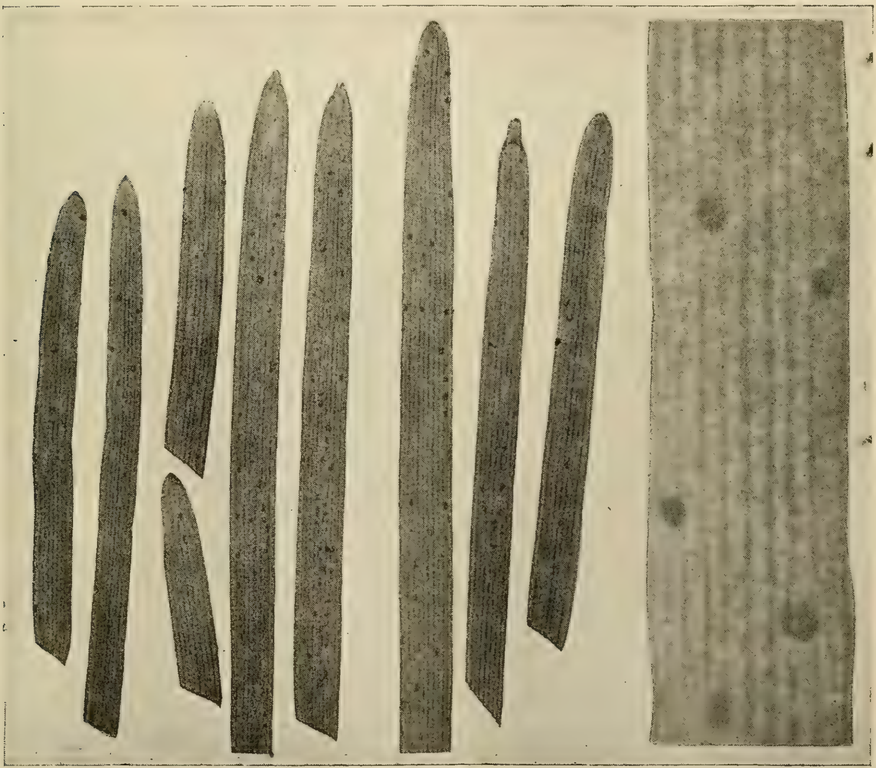

Fig. 2. Upper surface of rye leaves infected with *Puccinia rubigo-vera secalis,* and an enlargement just ten times the original size of one of these leaves.

PLATE XLI

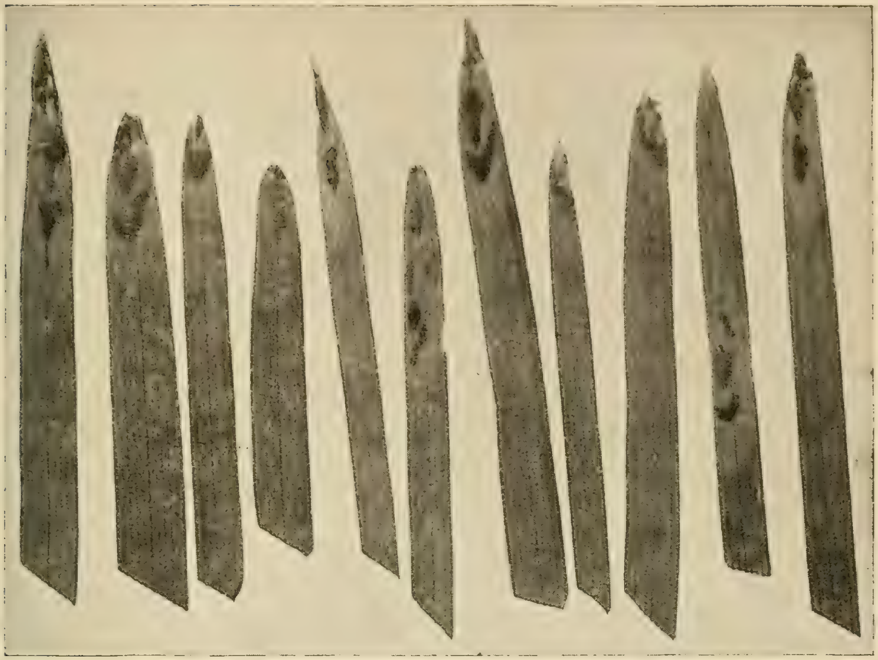

Fig. 1. Lower surface of wheat leaves infected with *Puccinia graminis tritici.* somewhat enlarged.

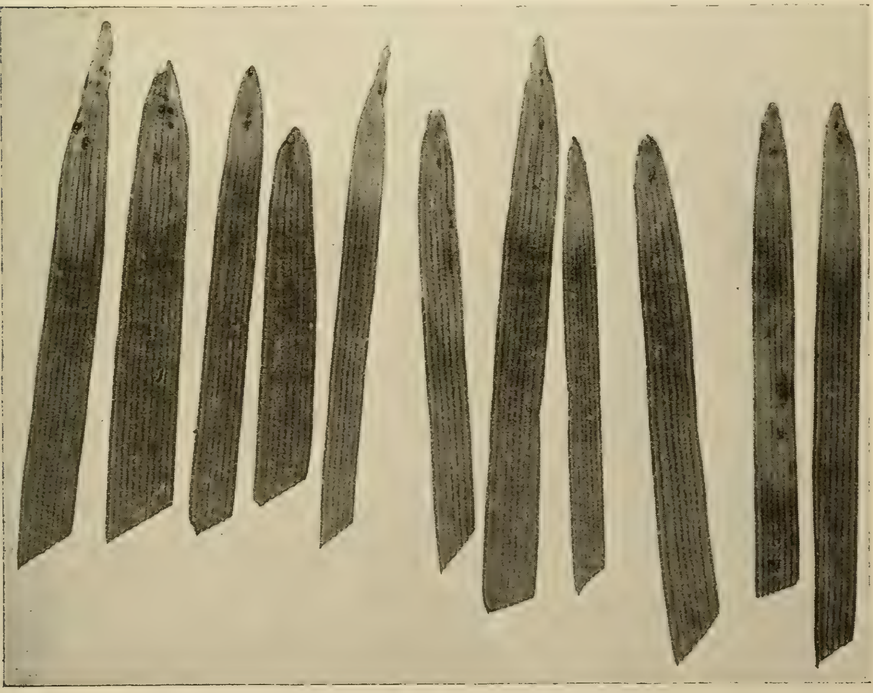

Fig. 2 Upper surface of the same leaves shown in figure 1.

PLATE XLII

RESPONSE OF MICRO-ORGANISMS TO COPPER SULPHATE TREATMENT

N. L. Huff

The object of this paper is to set forth the effect, upon several micro-organisms, of a series of copper sulphate treatments in Vadnais Lake during the summer of 1915. The lake was given three treatments during the summer: the first, June 14; the second, July 12; and the third, August 27. The study of the organisms was started on June 11, three days before the first treatment, and continued until the lake was frozen over on December 11, three and one-half months after the last treatment. Unless otherwise stated, the samples which furnished the material for the following results were collected just above the weir where the water, leaving Vadnais Lake, enters the conduit leading to McCarron Pumping Station.

Vadnais Lake is located seven miles north of the city of St. Paul, and has for the most part, high, well-drained shores. The lake is about one and three-fourths miles in length and one-third of a mile in width, covering about 358 acres. Its greatest depth is 57 feet, and the average depth for the entire lake is 27 feet.

The copper sulphate treatments were carried on by the Bureau of Water, Department of Public Utilities, of the City of St. Paul, for the purpose of destroying the micro-organisms which were objectionable in the city water supply. The writer wishes to acknowledge his indebtedness to this Bureau, and especially to Mr. G. O. House, General Superintendent, and Mr. R. L. Smith, Engineer, without whose assistance and coöperation the work would not have been possible.

The use of copper sulphate for eradicating algae and other objectionable organisms from storage reservoirs and city water sup-

plies has been practiced for more than ten years. The discovery by George T. Moore, in 1901, of the effect of copper sulphate upon *Spirogyra* in water-cress beds, and the publication by Moore and Kellerman of the Bureau of Plant Industry, U. S. Department of Agriculture, of a couple of bulletins[1] in 1904 and 1905, on the effect of copper sulphate upon bacteria and algae in water supplies, led to quite an extensive use of copper sulphate throughout the country. As early as 1905, the Journal of New England Water Works[2] gives a table, compiled from those who had used the copper sulphate treatment, showing the results of many experiments. This table contains definite information on several points, the size of the reservoir treated, the strength of the treatment, the name of one or more organisms causing trouble, and the general effect of the treatment upon the organism or organisms causing the trouble. The report covers some twenty-seven cities, representing more than a dozen different states. Both the strength of the treatment and the organism causing trouble varied a good deal in different places. The strength of the treatment was in most cases somewhere between 1 to 8,000,000 and 1 to 1,000,000, and the alga most frequently reported as causing trouble, was *Anabaena*. The results were almost uniformly favorable—destruction of the troublesome alga and disappearance of all disagreeable taste and odor from the water in a few days. In about one half of the cases cited the algae appeared again the same season, one, two, or three months after the treatment. In several cases where the algae did not occur again during the same season, the treatment was made rather late in the season, in August, September, October, or even as late as November, and the lateness of the season was doubtless largely responsible for their inability to get a second start.

Caird,[3] one of the early workers with the copper sulphate treatment, obtained some interesting results in treatment of reservoirs under normal conditions in 1904 and 1905, and gives in his reports the effect of several treatments of different strength, upon several algae common in the reservoirs treated.

Lovejoy's[4] experiments at Louisville in connection with filter troubles in 1909-10 are especially interesting. He found in 1909, when several organisms were clogging the filters, that by using 14 pounds of copper sulphate per million gallons of water, the filter runs were increased from two hours to the normal of twelve or

fourteen hours within three days after treatment. In August, 1910, when filter troubles were caused largely by *Synedra* and *Melosira* he found that a treatment of 1.67 parts per million increased the filter runs from about two hours to a normal of thirteen hours within three days after treatment.

While in many places the organisms to be destroyed have been determined before treatment, and the effects of the treatment upon one or more abundant organisms noted in a general way, in a very large number of cases where the treatment has been used, not even a microscopic examination of the water has been made and the species of algae present or causing the trouble were unknown. Definite and detailed reports giving the conditions under which treatments were made, the strength of the treatment, followed up by the results of the treatment upon various organisms, as can be determined only by regular and frequent microscopic counts of organisms present in the treated water, have in most cases been sadly neglected. The following paper shows the effect of copper sulphate upon several organisms common in Vadnais Lake.

The method used for determining the number of organisms is known as the Sedgwick-Rafter method, and may be described briefly as follows.

A sample consisting of 500 cubic centimeters of water is placed in a cylindrical funnel and filtered through a layer of fine sand about two centimeters in thickness. This sand strains out practically all organisms. When only 5 cubic centimeters of water remain unfiltered, the process is stopped, the sand and water are emptied out into a small beaker, and the sand thoroughly rinsed with this water, which is then carefully drained off into a clean beaker. The sand is rinsed again, this time with five cubic centimeters of distilled water, which removes practically all remaining organisms from the sand. The water used for this second rinsing is now mixed with that used for the first, and this is decanted two or three times to free it from all sand particles. This ten cubic centimeters is thoroughly mixed with a pipette, and while the organisms are still uniformly distributed throughout the mixture, a single cubic centimeter is removed and placed in the Sedgwick-Rafter counting cell, for microscopic examination. The Sedgwick-Rafter cell is exactly one millimeter in depth, and by proper ad-

justment of the draw-tube of the microscope, a Whipple eyepiece micrometer may be made to cover exactly one square millimeter. This will give as a field for counting, exactly one cubic millimeter, and makes the computation very simple. Usually ten counts were made from each sample, though when organisms were greatly reduced in numbers so that many cubic millimeters of the concentrated sample did not contain a single organism, one hundred such counts were made, in order to reduce as much as possible the error arising from the difficulty of picking out typical areas for the count. From the number of organisms found in a given volume of this concentrated sample it is a very simple matter to compute the number in the water as it is found in the lake.

On account of the great variation in size and form of different organisms, and the consequent impossibility of making comparisons between different organisms that would really mean anything, the figures used in the charts or diagrams for indicating the quantity of organisms present do not refer to the actual number of individuals or colonies of a given organism, but to standard units, a system of measurement suggested by Whipple for convenience in comparing the various forms. The standard unit is represented by a square 20 microns on a side (one micron equals 0.001 millimeter). In computing the number of standard units in a given individual or colony, an attempt has been made to approximate the volume rather than the area of the upper surface. In the majority of cases where individuals are quite uniform in size, the number of individuals was multiplied by a number found to be the average size for that species. In other cases, however, where there was great variation in size, as in filamentous forms, and forms growing in colonies of an indefinite size, the size was computed separately for each occurrence of the species in the part of the sample counted.

The method of distributing the copper sulphate in the lake was that which has commonly been employed in such treatments. About fifty pounds of the crystals were placed in a burlap sack, this tied to the stern of a boat and the boat rowed back and forth until the sulphate was dissolved, care being taken to distribute systematically, and as uniformly as possible. In addition to the rowboats which were used near the shore, a small motorboat with a bag of

copper sulphate attached to either side was used for distributing in the central part of the lake.

The following chemical analyses were made by Mr. V. H. Roehrich, Director of the Bureau of Municipal Testing Laboratories, Department of Public Utilities, of the City of St. Paul:

SAMPLE OF WATER TAKEN AT VADNAIS LAKE, AUGUST 13, 1915

Sanitary Analysis	Parts per million	Boiler Analysis	Parts per 100,000
Suspended matter	3.000	Total solids (dissolved)	16.50
Total solids (dissolved)	165.000	Total hardness	13.30
Chlorine	6.000	Sulphate hardness	.20
Nitrogen as free NH_3	.086	Total alkalinity	13.50
Nitrogen as albuminoid NH_3	.494	Alkali salts	3.00
Nitrogen as nitrites	.001	Sodium carbonate	.00
Nitrogen as nitrates	.480	Foaming rate	Very good
Oxygen consuming power	2.700	Incrusting rate	Very good

The following figures from Mr. Roehrich's report on the determination of copper in water taken from the terminal chamber at McCarron Pumping Station, four miles below Vadnais Lake, show how quickly the copper disappears from the water after a copper sulphate treatment:

About .03 parts of copper per million was introduced into Vadnais Lake at 11:00 a.m. on June 14, 1915.

	Parts of copper per million
Sample No. 1. Taken June 14, 1915 at 5:30 p.m.	.0005
Sample No. 2. Taken June 15, 1915 at 2:30 p.m.	.0175
Sample No. 3. Taken June 16, 1915 at 5:30 p.m.	.0015

As has been stated by Moore and others, it is impossible to give definite figures for the amount of copper sulphate necessary to eradicate a given organism, for several factors must be considered. The temperature of the water, the amount of organic matter present, as well as the presence or absence of various chemical substances such as calcium, magnesium, oxygen, and carbon dioxide, etc., probably have their effect upon the amount of copper sulphate necessary to destroy a given organism, and just what part each of these factors plays in the action of the copper sulphate upon algae, has not yet been determined. The figures, therefore, representing the quantity of copper sulphate necessary to eradi-

cate various organisms, vary a good deal with different observers. Moore and Kellerman (U. S. Department of Agriculture, Bureau of Plant Industry, *Bulletin 76,* 1905) give a table based in part upon treatments in reservoirs under normal conditions; Whipple (*The Microscopy of Drinking Water,* 255, 1914) gives a similar table, based largely upon Kellerman's figures. These are perhaps as reliable as any that have been compiled. The results of the treatment of Vadnais Lake, however, are so different from the results given by either of these observers, that it seems well worth while to direct our attention to a few of the organisms, and their response to the copper treatment here. One of the most interesting organisms in this connection is *Synedra pulchella.* Moore and Kellerman suggest for the eradication of *Synedra* the use of one part of copper sulphate in 600,000 parts of water. On June 14, the time of the first treatment with copper sulphate, there were present in the water at the weir as it enters the conduit leaving Vadnais Lake, 3,420 individuals of *Synedra pulchella* per cubic centimeter of water. The treatment given was about one part of copper sulphate to 12,000,000 parts of water, and by June 25, the number of *Synedra* had dropped from 3,420 to 1,116 per cubic centimeter. Other organisms present were reduced in a similar manner, but before a month had elapsed, practically all organisms were rapidly increasing again, and it was decided to give a second treatment. This time it was thought advisable to give a heavier treatment, so one part of copper sulphate was used for each 10,000,000 parts of water in the lake. This treatment was given on July 12, and *Synedra* had reached the very high figure of 7,720 individuals per cubic centimeter of water. The results of the heavier treatment were surprising. Each day showed a marked reduction in the number of *Synedra,* and in ten days' time the number had dropped from 7,720 to less than 100 individuals per cubic centimeter. For about four weeks following this, *Synedra* remained inactive, running from 12 or 15 per cubic centimeter to 100 per cubic centimeter, but not until about August 20 did they begin to show signs of rapid increase in numbers again. This remarkable reduction was secured by a treatment of one part in 10,000,000, or 6 per cent of that suggested by Moore and Kellerman as effective for *Synedra.* It is true that this treatment did not re-

sult in the complete destruction of *Synedra.* Whether this was due to certain hardy individuals that were able to withstand a treatment of that strength, or to the fact that the copper sulphate was not distributed with absolute uniformity and that some on this account escaped the treatment, we can not say. With these organisms pouring into the lake, however, in great quantities, as they were here through the waters of the inlet, it is doubtful if a treatment of several times this strength would have been effective for more than five or six weeks.

Among other organisms responding to a lighter treatment than that suggested by Moore and Kellerman, may be mentioned *Eudorina* and *Pandorina,* for which the above authors recommend the use of one part of copper sulphate to 100,000 parts of water, and *Stephanodiscus,* for which they recommend one part of copper sulphate to 250,000 parts of water. *Eudorina,* having 100 standard units per cubic centimeter of water, practically disappeared within five days after above treatment. *Pandorina,* with 162 standard units per cubic centimeter of water, dropped in eight days to an occasional single individual in a sample, and it was more than a month before either of these two organisms began to show any material increase in numbers. *Stephanodiscus,* which for nearly three weeks had maintained an average of 140 standard units per cubic centimeter of water, almost completely disappeared within a week after the second treatment, and only an occasional individual was found for several weeks following. Late in August a slight increase was noticed; but the third copper treatment was given about this time, and that put a check upon its development, and for more than another month it was unable to establish itself again. As samples were taken at several points in the lake, also from different depths in the deepest part of the lake, both before and after the treatment, and compared with samples taken daily at the weir, it was found that these figures may be considered not as representing the varying conditions of small local areas, but as essentially true for the entire lake surface, as well as for all depths down to twenty feet or more below the surface. Below a depth of twenty or twenty-five feet these and other algae were comparatively rare all summer.

About the twentieth of August, or more than a month after the

second treatment, the organisms, especially *Synedra,* began to show great increase in numbers. In seven days the total number of organisms increased from 100 standard units per cubic centimeter, to 3,952 standard units per cubic centimeter. A third treatment of copper sulphate on August 27, of the same strength as the second (1 to 10,000,000) given more than a month before, put a sudden check upon the increase, and brought them down, a little more slowly than before, but by the fourteenth of September they were again below 100 standard units per cubic centimeter and remained comparatively low for about another month, many of them not increasing again during the entire season.

During the summer months the water in the bottom of the lake has a temperature of from 10 to 20 degrees Fahrenheit lower than that of the surface. The maximum temperature for the bottom of the lake was about 59 degrees Fahrenheit, which was reached late in July. The surface temperature was sometimes as high as 78 degrees Fahrenheit. The colder, heavier water of the greater depth is not mixed with the lighter water above by ordinary surface disturbances, and therefore becomes quite stagnant during the several months when the surface water is comparatively warm. During September, however, with the short days and cooler nights, the water of the surface of the lake begins to cool and continues gradually until the lake freezes over in December. The water cools, of course, from the surface, and whenever the surface becomes cooler than the water of the bottom, this cooler, heavier surface water settles to the bottom, and the warmer water of the bottom rises to the surface. This circulation, or overturning process, will continue for several weeks until the temperature of all of the water in the lake has lowered to 39.2 degrees Fahrenheit, where it reaches its maximum density. In Vadnais Lake in 1915, this overturning process began about September 24, and continued until about November 25. In the early stages of this circulation, some organisms, especially diatoms, were more abundant at the bottom, fifty feet below the surface, than they were at the surface. During the greater part of the circulation period, however, the organisms were distributed nearly uniformly from surface to bottom of the lake. This was very different from their distribution during the summer months when the water near the bottom of the lake was

stagnant, and organisms in large numbers were never found below a depth of twenty or twenty-five feet.

The great increase of one species of diatom, *Stephanodiscus niagarae,* during the period of circulation, was not entirely unexpected. On the contrary, it seems a little strange that some of the other diatoms so common during the summer did not show a similar increase. It is generally known that diatoms increase during the period of circulation of water that follows a period of stagnation. Definite reasons for this phenomenon can not be given until we know the amounts of various materials, organic and inorganic, they require for food, as well as the conditions of temperature, light, and air most favorable to their growth and reproduction. It is known that some species of diatom are saprophytic,[5] and it is probable that many of them are able to utilize albuminous or similar nitrogenous compounds from the water in which they live. Dr. Maximilian Marsson[6] is authority for the statement that they can absorb carbon compounds from dissolved organic matter, also organic nitrogen, and when carbonic acid is excluded from the water in which they live, they can digest diluted volatile fatty acids, amido-acids, urea, peptone, and other substances. Karsten[7] found that certain diatoms not normally saprophytic could be made so by the proper cultivation in nutrient media. With this information on the food habits of diatoms, it is not difficult to see why the nutritive conditions in a lake like Vadnais are unusually favorable for these forms during the circulation period following several months of stagnation. The following theory for the explanation of the occurrence of maximum growths of diatoms during the circulation period following stagnation in deep lakes is offered by Whipple[8] and is well worth our attention here: With the decay of organic matter in the bottom, during the stagnation period, the water near the bottom undergoes great changes. Oxygen is exhausted, ammonia and other compounds, both organic and inorganic, increase and are dissolved in the water. With the upward currents during circulation, not only is this water, rich in food materials, carried upward where conditions for diatom growth are more favorable; but the spores, and the diatoms themselves,—which in their inactive condition, at least, are heavier than water and have lain dormant in the mud of the bottom, where light is too weak, and other conditions are unfavorable for growth,—are also carried upward where light and air

conditions are favorable, and with the abundant nourishment now present, they multiply with great rapidity. This perhaps accounts for the high point reached by some of the organisms, especially *Stephanodiscus,* late in the season while this autumnal shifting of waters was going on.

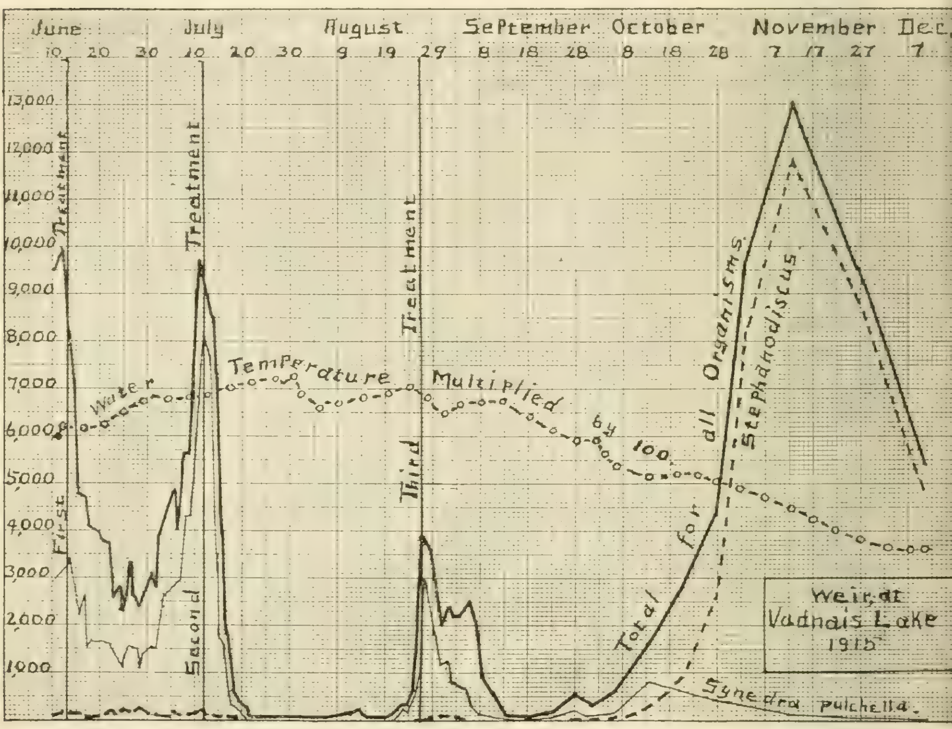

Fig. 1. General effects of copper sulphate upon the micro-organisms of Vadnais Lake.

A brief study of the accompanying charts or figures will give a much clearer idea of the effect of copper sulphate upon the various organisms than can be given perhaps in any other way. The variation in the total of all organisms from June 11 to December 11, is shown in figure 1. This chart shows also the variation of the two diatoms, *Synedra pulchella* and *Stephanodiscus niagarae,* the two most abundant organisms, as well as the changes in water temperature for the same period. On June 14, the day of the first treatment with copper sulphate, the total number of organisms per cubic centimeter of water was 8,100 standard units. Of these, 3,420 stan-

dard units were due to *Synedra pulchella*. The remaining 4,700 units were made up of other diatoms, green algae, blue-green algae, and protozoa, the numbers of which are brought out in other figures. The treatment consisted of about one part of copper sulphate to 12,000,000 parts of water. It was responded to by most of the forms, but was not nearly so effective as the slightly heavier treatments given later. Within less than two weeks the total number of organisms had dropped to 2,400, with about 1,100 standard units of *Synedra*. Early in July, *Synedra* began to show a rather rapid increase in numbers, and by July 12, had reached 8,260 standard units per cubic centimeter, bringing the total number of organisms per cubic centimeter up to approximately 9,700 standard units. A second treatment of one part of copper sulphate to 10,000,000 parts of water brought very decided and satisfactory results. Within ten days after the treatment the total number of organisms dropped from 9,700 to less than 100 per cubic centimeter, where they remained for more than four weeks.

The rate of increase or multiplication in some of the diatoms is interesting, and a glance at the chart (figure 1) will show how very rapidly they increase when once conditions become favorable for their growth. The following figures for *Synedra pulchella* show how it increased in eight days under normal conditions in Vadnais Lake:

Date	Individuals per cubic centimeter	Date	Individuals per cubic centimeter
August 19	46	" 24	225
" 20	80	" 25	520
" 21	114	" 26	1080
" 23	300	" 27	3020

Judging from these figures, *Synedra* may, under favorable conditions, double its number in about twenty-four hours, and at this rate of increase a comparatively small number surviving after the treatment, or entering the lake through the inlet after the treatment, will be sufficient to replenish the lake in a very short time.

On August 27, with the total number of organisms about 4,000 standard units per cubic centimeter, a third treatment of copper sulphate of the same strength as the second (1 to 10,000,000) was given the entire lake. The reduction of organisms that followed was similar to that of the second treatment, but required about eighteen days to bring the number below 100 standard units per cubic centimeter. *Synedra* and some of the other forms responded

much as before, but *Eudorina* and *Pandorina* continued to increase in numbers for several days after the treatment, and this accounts for the longer time required to bring down the total number to its former position. For more than a month following this reduction in numbers the total number of organisms did not rise above 1,000 standard units per cubic centimeter. The latter part of October, however, with the circulation following the stagnation period of the

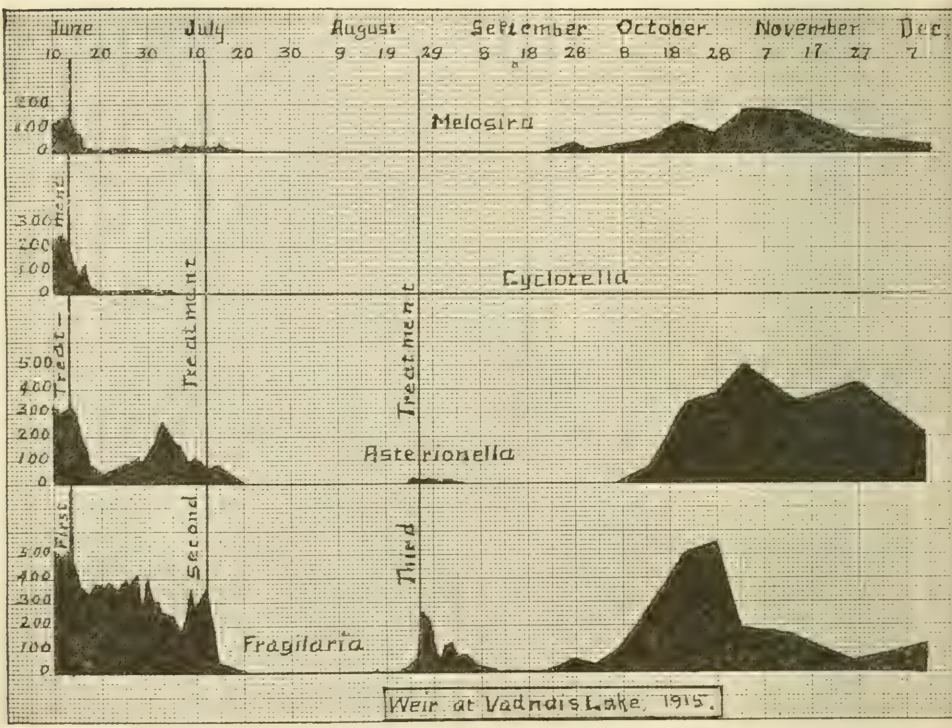

Fig. 2. Effect of copper sulphate upon certain diatoms.

summer months, some of the diatoms showed quite an increase. Most notable among these was *Stephanodiscus niagarae*, which continued to increase until about the middle of November, when it reached the very high number of 11,850 standard units per cubic centimeter. When the water temperature of the lake had lowered to 39.2 degrees Fahrenheit, the maximum density for water, and the circulation ceased, *Stephanodiscus* began to show a reduction in

numbers, and by December 11, about the time when the lake became frozen over for the winter, this organism had been reduced to about 4,920 standard units per cubic centimter, and was still going down very rapidly.

The response of four other diatoms to the copper sulphate treatments is shown in figure 2. These four, *Melosira granulata, Cyclotella comta, Asterionella formosa,* and *Fragilaria capucina,* were the only diatoms, aside from the two mentioned above, that occurred commonly in the main body of the lake. The first copper treatment resulted in the complete elimination of *Cyclotella comta* for the season. *Melosira,* which was greatly reduced by the first treatment, was practically eliminated by the second, not to occur in large numbers again until late in September, after the autumnal circulation had begun. *Asterionella* and *Fragilaria* were greatly reduced by the first treatment, and practically eliminated by the second treatment. Both of these had made a fair start, however, late in August, but the third treatment cut them down at this time and not until the autumnal circulation of late September and October, did they re-establish themselves in even fairly large numbers. These, like *Stephanodiscus,* were greatly reduced as soon as the autumnal circulation had ceased, and before the lake had started to freeze over.

The several species of green algae common in Vadnais Lake vary a good deal in their sensitiveness to copper sulphate. *Spirogyra,* for example, which was quite common, from 500 to 600 standard units per cubic centimeter at the time of the first treatment, was entirely eliminated within three or four days after the treatment. Just before the second treatment it occurred again in small quantities, there being from 100 to 150 standard units per cubic centimeter. With the second treatment it disappeared completely and not even a trace of it was found in the main body of the lake the remainder of the summer. Some other forms, however, especially *Eudorina* and *Pandorina* were found to be, at times, more resistant. These two forms, as is shown in figure 3, were running from 300 to 400 standard units per cubic centimeter at the time of the first treatment. They showed a decided decrease in numbers shortly after the treatment, but continued to oscillate a good deal between 50 and 300 standard units per cubic centimeter until after the second treatment, July 12. With this treatment both of these forms and two others, that had occurred in smaller numbers, namely *Pediastrum* and *Staurastrum,* were practically eliminated, none of them running

higher than from 1 to 10 standard units per cubic centimeter until late in August. The third treatment, August 27, was not responded to by *Eudorina* and *Pandorina* as quickly as the second treatment had been. Instead of decreasing at once as they had done before, they continued to increase slowly in numbers for about two weeks after the treatment. They were finally forced to succumb, however,

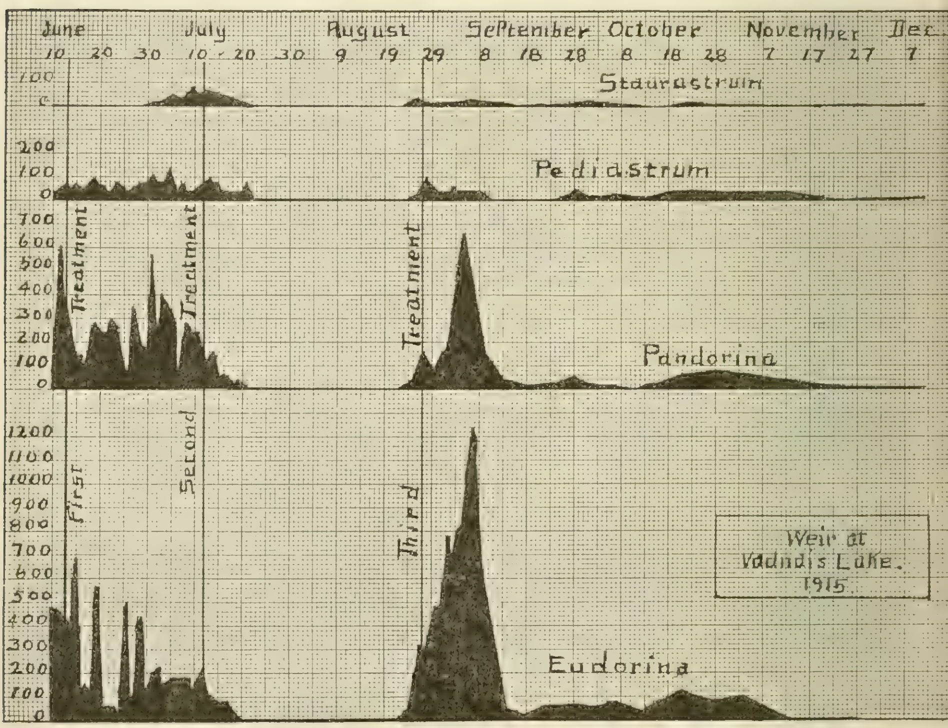

Fig. 3. Effect of copper sulphate upon certain green algae.

and after about two weeks of stubborn resistance, *Eudorina,* with 1,200, and *Pandorina,* with nearly 700 standard units, dropped rather suddenly to less than 100 standard units per cubic centimeter each. They did not rise materially again during the season.

Most of the blue-green algae are very sensitive to copper sulphate. At the time of the first treatment they were running from 1,500 to 2,000 standard units per cubic centimeter (figure 4), *Anabaena oscillarioides* being responsible for the greater part of this.

The first treatment cut the number down to an average of about 100 standard units per cubic centimeter, and the second treatment eliminated them almost completely. About the time of the third treatment they increased to 100 standard units per cubic centimeter, but were completely eliminated by this treatment, and scarcely a trace of them occurred again until late in October when *Aphanizomenon*

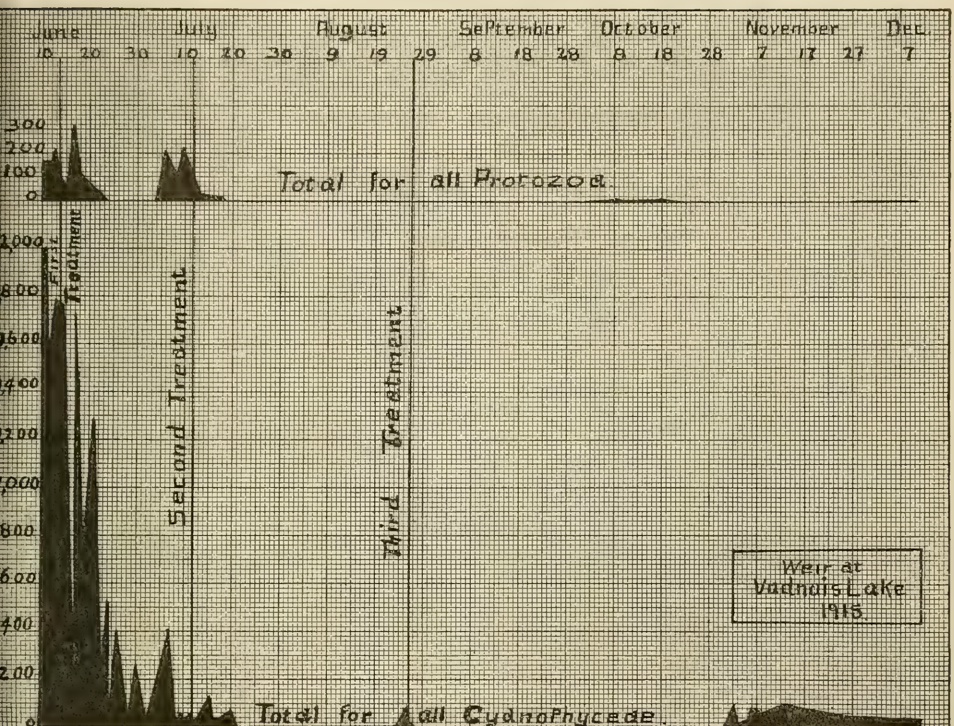

Fig. 4. Effect of copper sulphate upon certain blue-green algae and protozoa.

appeared, running at times to about 100 standard units per cubic centimeter, but never found in much larger numbers. Frequent application of small quantites of copper sulphate in a couple of small bays found to be favorite breeding places for blue-green algae doubtless helped materially in keeping these forms in check and prevented their spreading to other parts of the lake.

The only protozoa that were at all common at the weir where the water leaves the lake were *Ceratium, Dinobryon, Vorticella,* and *Uroglena.* The response of these forms to the copper treatment is

shown in figure 4. Running from about 200 to 300 standard units per cubic centimeter at the time of the first treatment, they disappeared for about ten days. They reappeared in similar numbers before the second treatment, but after the second treatment disappeared rather suddenly and only slight traces of them occurred again during the entire season.

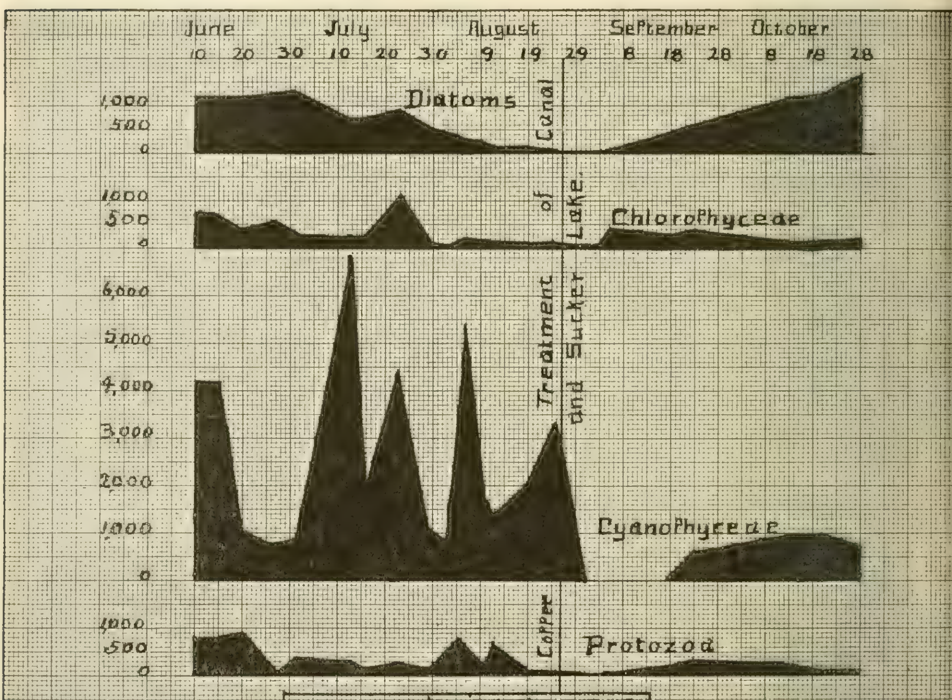

Fig. 5. Relative numbers of micro-organisms entering Vadnais Lake through waters of the inlet.

In order to get a better idea of the effect of copper sulphate upon the various organisms found in Vadnais Lake it may be well to compare the numbers of some groups entering the lake at the inlet (figure 5), with those in the water leaving the lake as indicated by figures 1 to 4. The two most abundant forms in Vadnais Lake, namely *Synedra pulchella* and *Stephanodiscus niagarae,* are forms that prefer the deep water, and while they enter the lake in small numbers, the explanation for the very large number occurring at

times in Vadnais Lake is to be sought in the conditions existing in this lake favorable to their growth and reproduction, rather than to any large number that may be found pouring into the lake at any one time through the inlet.

Of the four groups of organisms entering the lake, the *Cyanophyceae,* or blue-green algae, are usually most numerous, and appear to be, as a group, most sensitive to the copper sulphate. For about ten weeks during the summer, they ran from 1,000 to 7,000 standard units per cubic centimeter at the inlet, with an average for this period of about of about 2,500 standard units per cubic centimeter. At the outlet of the lake they were running about 2,000 standard units per cubic centimeter at the beginning of this period, but after the first treatment they rapidly disappeared and during the last six weeks of this period scarcely a trace of them was found. On August 27, at the time of the third treatment of Vadnais Lake, the creek entering the lake, and Sucker Lake, a small lake a short distance above Vadnais, were treated, and for the first time during the summer the organisms practically disappeared from the waters of the inlet. Although the treatment here was considerably heavier than in Vadnais Lake, the effects were of shorter duration, for the smaller size of Sucker Lake and the creek permits a more rapid displacement of the treated water by untreated water from above.

From the tenth of June to the twenty-seventh of August, the average number of organisms in the inlet of Vadnais Lake was more than 4,000 standard units per cubic centimeter. Compare these figures with the number found in the samples taken at the weir below the gatehouse, especially for a period of about five or six weeks following the copper sulphate treatments of the lake, when the number here was below 100 standard units per cubic centimeter, and the effectiveness of a treatment of 1 to 10,000,000 can not be questioned.

While many organisms appeared at one time or another during the summer in the waters of Vadnais Lake, and disappeared, probably as a result of the copper treatment, many of them were not found in sufficiently large numbers to justify a statement concerning the exact effect of copper sulphate upon their existence. With several others, however, that were more common, there can be no question as to the effect of copper sulphate. The following forms were found before one or more of the treatments, in sufficient numbers to justify certain conclusions concerning the effects of the treatment as here given.

Chlorophyceae
Spirogyra sp.
Eudorina elegans Ehr.
Pandorina morum (Müll.) Bory.
Pediastrum duplex Meyen.
Staurastrum sp.

Diatomaceae
Stephanodiscus niagarae Ehr.
Synedra pulchella (Ralfs.) Kg.
Fragilaria capucina Desmaz.
Asterionella formosa Hass.
Cyclotella comta (Ehr.) Kg.
Melosira granulata (Ehr.) Ralfs.

Cyanophyceae
Anabaena oscillarioides Bory.
Anabaena flos-aquae (Lyngb.) Bréb.
Clathrocystis aeruginosa (Kuetzing) Henfrey
Coelosphaerium kuetzingianum Naegeli.
Aphanizomenon flos-aquae (Linn.) Ralfs.
Rivularia echinulata (Smith) Born. and Flah.

Protozoa
Ceratium longicorne Carter
Dinobryon sertularia Ehr.
Uroglena volvox Ehr.
Vorticella communis Ehr.

From observations made on the above-mentioned forms, the results of which are for the most part shown in accompanying diagrams or figures, the following conclusions may be drawn:

1. With the conditions under which the treatments were made, the use of one part of copper sulphate in 12,000,000 parts of water is quite adequate for the elimination of *Spirogyra*, *Cyclotella*, and most of the *Cyanophyceae*. It will practically eliminate *Melosira* and the four protozoa here listed; for the other forms mentioned it will bring about great reduction, but may not eliminate them.

2. The use of one part of copper sulphate in 10,000,000 parts of water is effective in practically eliminating all forms mentioned in the list, with the possible exception of *Eudorina* and *Pandorina*, and with the conditions under which the treatments were made, this amount is entirely adequate for their suppression.

3. With the conditions under which the treatments were made, a treatment of one part of copper sulphate in 10,000,000 parts of water remains effective for about five weeks, after which time the organisms present, or many of them at least, seem to find conditions favorable for their growth and reproduction, and if the treatment is not repeated at this time they may increase again with remarkable rapidity.

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STUDIES IN THE MORPHOLOGY OF YUCCA GLAUCA

DONALD FOLSOM

INTRODUCTION

Yucca glauca—whose general appearance is shown in plates XXVIII, XXXIV—was first described by Nuttall in 1813, and later as *Yucca angustifolia* by Pursh in 1814.[4] A comprehensive discussion of the taxonomy and nomenclature of the Yucceae, a tribe of the Lilaceae, has been given by Trelease.[4] An account of the chemical nature of *Yucca glauca* was published by Abbott in 1887.[2] The following studies are based upon data and material secured in the sandhill region of Nebraska in June and July of 1912. The ecological aspects of this region, in parts of which *Yucca glauca* is very prominent, have been described by Pool.[7,8] The writer is under obligations to Professor Pool for helpful suggestions and aid in photography received while with him during the summer of 1912, and to Professors Clements, Rosendahl, and Butters, for suggestions and advice received during the preparation of this paper.

TECHNIQUE

Most of the material was obtained near the Forest Reserve, Halsey, Nebraska; some—immature seeds—near Hackberry Lake in Cherry County. All of it was killed and fixed in a chrom-acetic solution made up as follows:

Chromic acid	2.5 grams
Glacial acetic acid	10.0 cc.
Well water	1000.0 cc.

This fixing fluid apparently did not combine the reagents in the right proportion, for it often caused more or less plasmolysis in

actively growing tissues and usually produced excessive shrinking in the embryo sac. The usual paraffin method, with xylol as a clearing agent, was used in making the preparations. The sections, which were from 4 mic. to 10 mic. in thickness, were stained best by Haidenhain's iron-alum haematoxylin and by the triple stain—anilin-water safranin, gentian violet, and orange G— used according to Harper's short method. Drawings were made with the aid of an Abbé camera lucida using a Bausch and Lomb microscope, a combination of a 1.9 mm. "semi-apochromatic" oil-immersion lens and a No. 12 compensating Zeiss ocular, and other combinations giving less magnification.

General Development of Ovule and Embryo Sac

The youngest ovaries examined contain in each an axial six-rayed cavity which becomes closed by the almost complete growing together of the three carpels (Plate XLIII, fig. 13). Thus three loculi are formed whose upper ends unite just above the ovuliferous portion to form an open tube ending in the center of the stigma. In each loculus two rows of ovules begin to protrude from the placentae (fig. 13).

While the ovule is becoming inverted, the inner integument pushes out, followed by the outer (fig. 16). These elongate—the outer one also increasing considerably in thickness—until at anthesis they completely enclose the nucellus except for the rather open micropyle (fig. 19; fig. 24, ovule .45 mm. long; fig. 31; fig. 35, ovule .93 mm. long). After fertilization the growth of the integuments continues, accompanying the growth of the embryo sac (fig. 38, ovule 4 mm. long; fig. 40, ovule 8 mm. long), the micropyle becoming closed entirely in six to eight days.

When the integuments have become nearly as long as the nucellus, the latter contains a cylindrical to ovoid group of megaspores (figs. 20-21, group 63 mic. x 35 mic.; fig. 22). The embryo sac soon comes to fill the whole space formerly occupied by this group of megaspores. It grows uniformly in length during the entire development of the ovule until it reaches its mature size in the nearly ripe seed. For a time it maintains a nearly proportional growth in all dimensions, but some time before anthesis its growth in width gradually ceases at the chalazal end while continuing in the more distal portion. As a result the embryo sac becomes first more or less

wedge-shaped (figs. 27, 29), and later, a short time before anthesis, club-shaped with a narrow antipodal portion (fig. 30, 55 mic. x 30 mic.) and an enlarged micropylar portion (fig. 30, 145 mic. x 110 mic.) Disintegration of part of the nucellar tissue around the micropylar end of the embryo sac begins with the first stages in the formation of the embryo sac and is complete at the time of flowering (figs. 25-30).

Ovule Previous to Fertilization

When the rudiment of the ovule protrudes from the placenta, an archesporial cell is differentiated (fig. 14), being larger than the other cells, just below the epidermis at the distal end of the nucellus. The archesporial cell divides periclinally into a small tapetal cell and a large megaspore mother-cell (fig. 15). The former later divides once or twice anticlinally. The latter increases in size (fig. 16) and goes through two successive divisions, giving rise to four megaspores by the time the integuments have become as long as the nucellus (figs. 17-21). The somatic number of chromosomes, twelve, is reduced to six in the first of these mitoses (figs. 17-18).

There are three general types of arrangement of the megaspores. All four may lie in a row in the axis of the nucellus or either the two micropylar megaspores or the two middle ones may be side by side. In the latter cases the two which lie side by side appear to have no definite orientation in respect to the axis of the ovary, as in cross-sections of the ovary they sometimes appear in the same plane, and sometimes with one directly or obliquely behind the other. The most common type of arrangement is the second. The relative frequency of occurrence of the three types may be seen in table I.

Three of the megaspores break down (figs. 22, 23), while the fourth develops into the embryo sac. The functional spore may be any one of the group, and about an equal number of instances were observed in which the distal, a proximal, or one of the central spores, respectively, were developing (see table I). The functional megaspore (figs. 23-25) germinates in the usual way, forming eight nuclei by three successive divisions, of which the second and third occur near the poles of the embryo sac (figs. 26-28). The fusion of the two polar nuclei takes place near the antipodal end of the embryo sac before the flowers open (fig. 30).

Pollen and Pollen Tubes

A cross-section of an anther shows four pollen sacs, each having an epidermal layer, an endothecium, one middle layer, and a tapetal layer. The tapetal cells, which have from one to three nuclei in each, break down before the time of pollination. The pollen mother-cells are in synapsis at the time when the ovules first appear (figs. 1-2). The somatic number of chromosomes, twelve, is reduced to six probably in the first mitosis of the pollen mother-cell; unfortunately the metaphase of this mitosis was not available. Six chromosomes appear at each pole of the heterotypic diaster (fig. 4) and in the homotypic metaphase (figs. 5-8). Each mitosis is followed immediately by the development of a cell wall so that the mother-cell is first divided into two hemispherical daughter cells and then into four bilateral grand-daughter cells. These two second dividing walls may meet each other at any angle. The pollen grains soon become separated. The nucleus (fig. 10) divides before pollination (fig. 11), and the grain becomes shaped like a shortened wheat kernel.

The night-blooming flowers open at sunset, each flower opening on several successive evenings. They are pollinated within a few hours after the flower opens. Their pollination by the moth *Pronuba yuccasella* has been carefully observed by Riley.[3] The mass of pollen is deposited in the end of a tube in the center of the stigma and there the pollen grains germinate before sunrise. Within two to four days after pollination, the pollen tubes grow down through the open stigmatic tube, through its three branches which lead to the three cavities of the ovary, along the placentae and the funiculi of the ovules, and through the micropyles. They pass through a granular substance filling the micropyle and covering the adjacent part of the funiculus (fig. 31). This substance is seen from just before anthesis until the pollen tube reaches the embryo sac, and may contain chemotactic substances which direct the course of the tube; a similar condition in *Yucca filamentosa* L. is reported by Reed.[5] The tube usually decreases in diameter as it pierces the layer of nucellar cells, and discharges its contents into the embryo sac without going beyond this layer (figs. 33, 34).

Fertilization

Two ellipsoidal male nuclei are discharged from the pollen tube

(fig. 33). In several instances only one was seen and then it was observed to be either between the egg and definitive nucleus or in process of uniting with the latter; probably in these cases fusion of the other male nucleus with the egg had already taken place. Although the latter fusion was not observed, double fertilization is indicated by the fact that mitoses in somatic and endosperm cells show respectively twelve and eighteen chromosomes, twice and three times the haploid number.

Ovule After Fertilization

When the pollen tube enters the embryo sac, one of the synergids disintegrates (figs. 32, 33), while the other persists (fig. 34) until the proembryo is formed. After fertilization, walls are distinctly seen around the antipodal cells, whose nuclei begin to disintegrate before fertilization (fig. 30) and continue to do so afterwards (fig. 32), but have not entirely disappeared even when the young embryo is formed. Evidently double fertilization is soon followed by a division of the definitive nucleus, for in the many cases observed (see table I) where the pollen tube had entered the embryo sac and the male nuclei were no longer to be seen, the definite nucleus had divided to begin the formation of free endosperm nuclei (figs. 36, 37). Walls appear between these after the formation of the embryo (fig. 39).

The fertilized egg remains dormant for about four days (fig. 34). Then it divides and a proembryo is formed (figs. 36-38), consisting finally of a row of from four to eight cells, the basal one usually being larger than any other but sometimes becoming divided by an oblique wall after two or more divisions of the egg. In the most mature ovules obtained, the suspensor consists of a row of four to eight cells and the young embryo is ovoid with two rather flat surfaces parallel to the two broad faces of the seed, one of these surfaces containing a slight depression (figs. 39, 40, 42, 43).

Comparisons with Observations on Other Species of Yucca

The somatic number of chromosomes is twelve and they are all uniform in size, while in *Yucca aloifolia* L., *Y. Draconis* Torr., and *Y. guatemalensis* L., Müller reports ten large and many small ones.[6] In *Yucca filamentosa* L. the tapetal cells are like the megaspores

in shape and size, according to Reed,[4] while in *Yucca glauca* the latter are distinguished from the former by their greater size, fewer and larger nucleoli, less dense nuclear contents, and greater tendency to plasmolyze (fig. 21). Also, in *Y. filamentosa* the second and third divisions in the germination of the functional megaspore occur at the antipodal end (Reed[4]), but in *Y. glauca* they occur at the two ends (figs. 25-29).

TABLE I

RECORD OF NUMBER OF TIMES THAT EACH IMPORTANT STAGE WAS OBSERVED

Kind of Structure	Number of structures seen in the stage	Number of flowers from which the structures came
Ovule with hypodermal initial cell	m*	5
" " initial divided	m	10
" " spore mother-cell enlarging and integuments evident	m	12
" " reduction division	33	6
Preceding with number of chromosomes evident	4	3
Ovule with four megaspores	101	10
All in one row	16	5
Micropylar pair side by side	64	7
Middle ones side by side	12	5
Ovule with three megaspores during or after disintegration	52	7
Functional megaspore at antipodal end	14	5
" " at micropylar end	12	3
" " in middle	13	5
Embryo sac with two nuclei	56	5
" " " four "	95	6
" " " eight "	12	3
" " " two polar nuclei fusing or about to fuse at chalazal end	21	4
Embryo sac with seven nuclei	85	8
Pollen reduction-division prophases	m	8
" " " metaphases	m	2
" " " telophases	6	2
Pollen grains grouped by fours	m	6
" " separate, one-nucleate	m	14
" " two-nucleate	m	1
" " after germination	m	7
Embryo sac with two male nuclei	3	3
" " " one male nucleus, before or during its fusion with fusion nucleus	4	2
Embryo sac with pollen tube, free endosperm nuclei, and egg undivided	94	10
Embryo sac with proembryo	30	6
" " " walled endosperm cells and embryo	11	5
Mitosis of sporophyte cell with twelve chromosomes evident	23	1
" " endosperm cell with 18 chromosomes evident	20	2
With at least 15 and possibly 18	27	2

*m=many in each flower.

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EXPLANATION OF PLATES

PLATE XLIII

Figures 1-9. Stages in reduction division of pollen mother cell. × 700.
1. Before synapsis.
2. Synapsis.
3. Late prophase, after synapsis.
4. Homotypic prophase and half of heterotypic diaster.
5. Two homotypic metaphases, each showing six chromosomes.

6-8. Homotypic metaphase with six chromosomes.

9. Homotypic anaphase.
10. End view of one-nucleate pollen grain. × 700.
11. Side view of two-nucleate pollen grain. × 300.
12. Pollen grain and part of pollen tube on stigma sixteen hours after opening of flower. × 300.
13. Cross-section of young ovary. × 28.
14. Ovule (a of fig. 13) with archesporial cell in detail. × 700.
15. Tip of ovule with tapetal cell and megaspore mother-cell in detail. × 700.
16. Tip of ovule with megaspore mother-cell in detail. × 700.
17. Tip of ovule with metaphase of heterotypic division of megaspore mother-cell. × 300.
18. Chromosomes (in outline) and spindle fibers of preceding. × 1225.
19. Cross-section of loculus: a, ovule containing four megaspores. × 72.

PLATE XLIV

20. Ovule a of preceding. × 300.
21. Four megaspores and a nucellar cell of preceding in detail. × 700.
22. Megaspores in detail, during breaking down of some. × 700.
23. Part of nucellus with functional megaspore in detail, remnants of three others, and tapetal cells beginning to break down. × 700.
24. Ovule containing the preceding. × 72.
25. Part of nucellus of preceding. × 300.
26. Part of nucellus after first division of functional megaspore. × 300.
27. Part of nucellus with tapetal layer disintegrated. × 300.
28. Metaphase in polar view in nucellar cell of preceding; twelve chromosomes in outline. × 1225.
29. Embryo sac with eight nuclei. × 300.

PLATE XLV

30. Embryo sac during fusion of polar nuclei near chalazal end. × 300.
31. Ovule containing preceding: a, layer probably containing substances which direct growth of pollen tube. × 72.

32. Embryo sac after discharge of male nuclei and before double fertilization: f, fusion nucleus. × 300.
33. Micropylar end of preceding: e, egg apparatus; m, male nuclei; n, nucellus (diagrammatic). × 1225.
34. Micropylar end of embryo sac after fertilization: e, egg; s, synergid. × 700.
35. Ovule containing preceding. × 72.

PLATE XLVI

36. Micropylar end of embryo sac containing proembryo and one endosperm nucleus; nucellus diagrammatic. × 300.
37. Embryo sac containing preceding. × 45.
38. Cross-section of carpel: e, embryo sac of fig. 37. × 2½.
39. Embryo surrounded by endosperm tissue with walls. × 300.
40. Full-sized ovule containing embryo in stage of preceding: e, embryo sac. × 2½.
41. Outlines of thirty-six chromosomes in anaphase in endosperm cell of preceding. × 1225.
42. Long-section of embryo from full-sized ovule: n, nucellus. × 72.
43. Cross-section of embryo from full-sized ovule: n, nucellus. × 72.

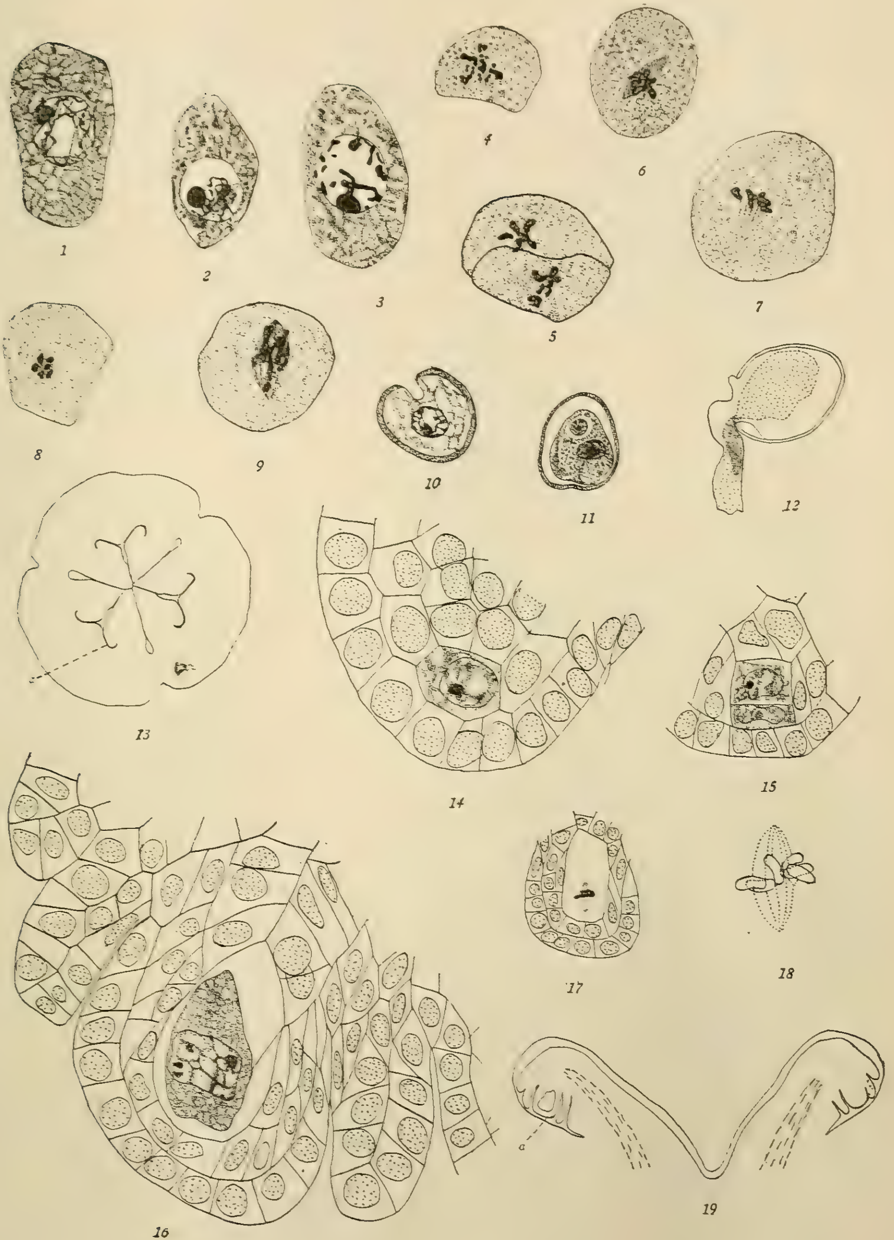
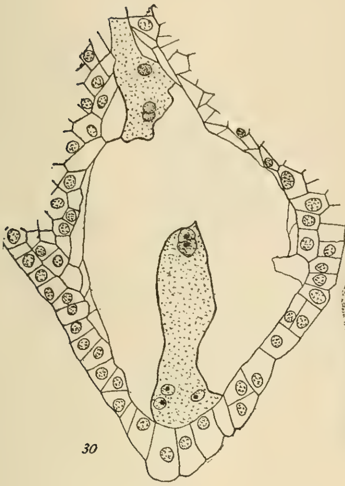


PLATE XLIII



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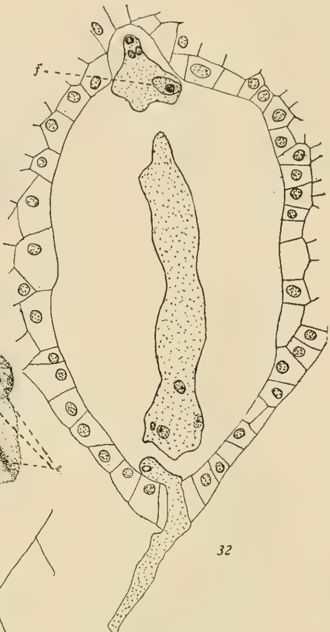

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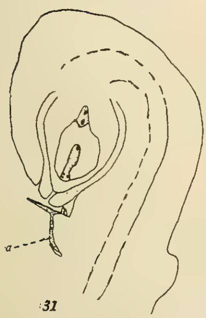

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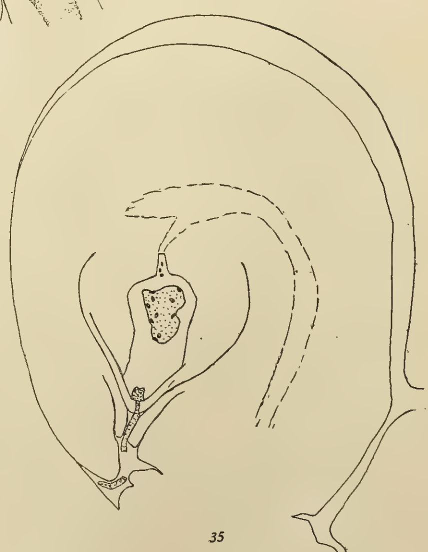

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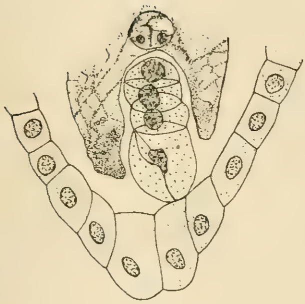
PLATE XLV



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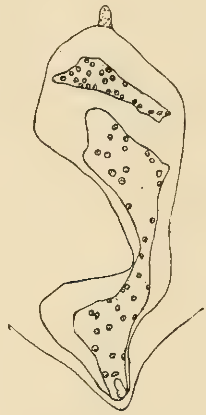

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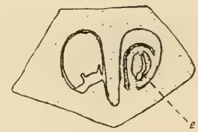

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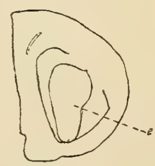

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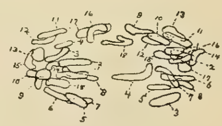

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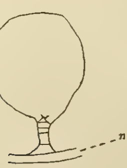

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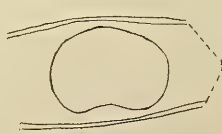

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PLATE XLVI

COMMENTS ON MALVA ROTUNDIFOLIA L. AND ITS ALLIES

H. F. Bergman

There has been some confusion as to the identity of *M. rotundifolia* L., and some of its related forms as becomes apparent by a careful study of herbarium specimens and by an analysis of descriptions in manuals. *M. rotundifolia* L., and *M. borealis* Wallm., are easily confused because of great similarity, but *M. borealis* and *M. parviflora* L., are confused frequently also, although quite diverse in character.

In part, this confusion is due to the incompleteness of the descriptions of these species, the difference in size of flowers, number of carpels, markings and pubescence of carpels, if observed, having been regarded as variations unworthy of recognition. However, there are definite correlations of characters distinguishing each species, a fact that has long been recognized by European botanists.

Just what Linné's type of *Malva rotundifolia* may have been is uncertain, but European botanists agree well on the characterization of the species. Although it appears often in literature under the names *M. neglecta* Wallr., and *M. vulgaris* Fr., the identity of these with *M. rotundifolia* is evident from the descriptions, and is also established by the frequent citation of these as synonyms of *M. rotundifolia.*

M. borealis Wallm., is often mistaken for *M. rotundifolia,* and, although the species seem to have been quite generally recognized in European manuals, there has been difficulty in the correct application of names. Blytt, in *Norges Flora* 3: 1077, describes both *M. rotundifolia* and *M. borealis,* and points out carefully the distinction between them as follows: "From the following, it [*M. rotundifolia*] is separated by the following characters: The involucral bracts linear-lanceolate, shorter than the sepals which are stellate-pubescent as is also the pedicel. Petals white or pink with darker veins,

emarginate, almost ½ inch long, 2-3 times as long as the calyx. Carpels 12-15, finely pubescent, smooth (not wrinkled), with rounded edges."

He gives the following description of *M. borealis* Wallm.: "Stems ½-2 feet long, prostrate or ascending, leaves reniform-orbicular, 5-7-lobed with rounded lobes or obscurely digitate. Pedicels after blooming reflexed, in clusters in axils of the leaves. Involucral leaves linear about as long as the broadly ovate, at last net-veined, ciliate-margined calyx-lobes. Petals small, white, emarginate, of the same length as the calyx. Carpels 10, reticulate, with sharp edges, somewhat hairy. Plant with spreading hairs."

A good brief characterization of *M. rotundifolia* L., and *M. parviflora* L., with figures, is to be found in Bonnier and Layens, *Flore Complete de la France et de la Suisse,* page 55.

Ledebour, in *Flora Rossica,* 1 : 345, gives all three species with very good descriptions and synonymy. The following table shows the differences between the three species.

	M. rotundifolia	*M. borealis*	*M. parviflora*
Habit	Prostrate or ascending	Prostrate or sometimes erect	Erect or in dwarfed plants prostrate or ascending
Leaves	5-7-lobed, the lobes rounded.	5-7-lobed, the lobes rounded or angular	5-7-lobed, the lobes rounded or angular
Pubescence	Stellate, often dense or plant sometimes glabrate.	Simple or branched rarely stellate, usually spreading.	Stellate, often dense or plant becoming glabrate.
Calyx	Enclosing the fruit, never spreading; sepals lance-ovate, acuminate, stellate pubescent, often densely so, not ciliate on the margins or only slightly.	Ascending or enclosing the fruit, usually not conspicuously veiny; sepals lance-ovate, acuminate, the margins long ciliate, glabrous or pubescent with simple or sometimes branched spreading hairs.	Usually widely spreading, very veiny; sepals broadly ovate, acute, the margins not ciliate, usually stellate pubescent, often densely so.
Petals	3-4 times the length of the sepals.	As long as or slightly longer than the sepals.	One and one-half to twice the length of the sepals.
Carpels	12-15; backs pubescent with short hairs, usually densely so, not at all or very faintly reticulated; margins rounded.	8-11 (usually 10); backs conspicuously reticulated, pubescence scant or none; margins angled and sometimes slightly toothed.	8-11 (usually 10); the backs strongly transversely ridged and reticulated, somewhat pubescent, never densely so; margins sharply angled and often toothed.

The characters here enumerated, for the most part, are to be found in descriptions as given in European manuals. These have been checked by careful study of a large number of specimens from different parts of the world.

Referring to American manuals, we find in Gray's *Manual*, 7th edition, that *M. rotundifolia* is the only species mentioned. Britton & Brown, *Illustrated Flora*, ed. 3, add *M. parviflora*.

Specimens of *M. borealis* have been collected from New Jersey, Pennsylvania, and Michigan as indicated below, and it seems that this species must have been introduced and have become established at other points in the east. A single specimen, too young for certain identification, but apparently *M. borealis*, was collected at Ames, Iowa, by J. R. Campbell. *M. borealis* occurs in the Red River Valley in North Dakota and probably also on the Minnesota side. *M. borealis* has been collected at other points in North Dakota, as has also *M. parviflora*. From this it is evident that both manuals used generally in northeastern United States should include all three species.

In the Rocky Mountain region, Rydberg, in the *Flora of Colorado*, includes *M. rotundifolia* and *M. parviflora*, while Nelson, in the *New Manual of the Rocky Mountains*, describes only the former, although Colorado is within the region covered. Both *M. parviflora* and *M. borealis* occur within the range of Nelson's manual, and should be included therein. The confusion of *M. borealis* with *M. rotundifolia* may account for the failure to include the former. *M. borealis* occurs in Montana, Wyoming, and Colorado. *M. parviflora* has been collected in Wyoming, and is reported also from Montana in Rydberg's *Flora of Montana*.

References to the manuals of the Pacific Coast region reveal some interesting things. Brewer and Watson in the *Geological Survey of California*, 83, describe *M. borealis* Wallm., but it is apparent from the description that the plant described is not *M. borealis* of Wallman but *M. parviflora* L. The erect habit, enlarged calyx, and transversely rugose-reticulate carpels are peculiar to the latter species. *M. borealis* is seldom erect, the calyx does not become enlarged in fruit, and the carpels are not transversely rugose-reticulate.

Howell, in the *Flora of Northwestern North America*, 100,

makes the same error. The description is that of *M. parviflora* L., and not of *M. borealis* Wallm.

Piper, in the *Flora of Washington,* mentions only *M. rotundifolia,* although *M. parviflora* is included by Howell as above mentioned.

Greene, in the *Manual of the Botany of the San Francisco Bay Region,* 64, gives a correct characterization of both *M. parviflora* and *M. borealis,* but does not mention *M. rotundifolia.* The latter is known to occur in California, but possibly not in the area covered by Greene.

It is of interest here to note erroneous determinations of specimens from several of the larger herbaria in the United States. The following are specimens of *M. rotundifolia* that have been confused with and distributed under the name of *M. borealis:*

Klamath River, Cal. Chandler 1405.
Mt. Shasta, Siskyou Co., Cal. H. E. Brown, June, 1897.
Provo, Utah. M. E. Jones 5501, June 25, 1894.
Vancouver, Wash. E. P. Sheldon 13035, October 18, 1903.
Milton, Umatilla Co., Ore. H. E. Brown 36, August 26, 1893.

The following specimens of *M. rotundifolia* have been erroneously determined as *M. parviflora* and distributed as such:

Boulder, Colo. Frank Tweedy 4974, July, 1902.
Bay Farm Island, Cal. J. Burt Davy, September 24, 1898.
Leeds, North Dakota. J. Lunell, July 30, 1904.

The following are specimens of *M. borealis* which have been collected and distributed as *M. rotundifolia:*

Limestone, Crook Co., Wyo. A. Nelson 9532.
Leeds, North Dakota. J. Lunell, August 1, 1899.
Turin, Marquette Co., Mich. Bronson Barlow, August 28, 1901.

Specimens of *M. borealis* correctly labelled have been collected from the following places:

Philadelphia, Pa. Isaac C. Martindale, August, 1880.
Kaign's Point, N. J. Ex Herb. Isaac Burke, Phila.
Camden, N. J. Isaac C. Martindale, 1879.
Brazos, Santiago, Texas, G. C. Neally 34, 1889.
Old San Bernardino, Cal. S. B. Parish 2057, May, 1891.
San Louis Obispo Co., Cal. Geo. B. Grant 746, April, 1903.
Stockton, Cal. J. A. Sanford, 1890-91.
Humboldt Co., Cal. C. C. Marshall, 1888.
Alton, Humboldt Co., Cal. J. P. Tracy 3687, June, 1912.

The following specimens of *M. borealis* have been collected and distributed as *M. parviflora:*

Thompson Falls, Mont. J. W. Blankinship, August 6, 1901.
Willows, Colusa Co., Cal. J. Burt Davy, May, 1898.

The following specimens collected and distributed as *M. borealis* are incorrectly named and should be referred to *M. parviflora:*

San Diego, Cal. Dr. J. G. Cooper 435, March 7, 1862.
San Louis Obispo, Co., Cal. Mrs. R. W. Summers, 1886.
San Nicholas Island, Cal. Blanche Traske, April, 1897.
Santa Barbara, Cal. W. H. Brewer 306, March, 1861.
Tempe, Ariz. D. Griffiths 4329.
Tuscon, Ariz. D. Griffiths 3471.
Tuscon, Ariz. J. W. Tuomey 79, March 19, 1892.
Tuscon, Ariz. Thornber 459, April 16, 1904.
Verde Mesa, Ariz. D. Smart 242, 1867.
Phoenix, Ariz. L. H. Dewey, June 19, 1891.
Santa Fe, N. M. A. Isabel Mulford 1282.

These errors were found among specimens loaned from the U. S. National Herbarium; Gray Herbarium, Harvard; Field Columbian Museum, Chicago; Herbarium of the Shaw Botanical Garden, St. Louis; Herbarium of the University of California; Herbarium of the University of Wyoming; and from the Herbarium of the Arizona Experiment Station, Tucson. These specimens represented collections from all parts of the United States, Mexico, South America, Europe, Asia and a few specimens from Africa. The foreign specimens were used in establishing the identity of the three species studied and as standards of comparison for specimens from the United States.

Grateful acknowledgment is made to the curators of the herbaria above named for the loan of collections and to Dr. C. O. Rosendahl, of the University of Minnesota, for securing these loans.

EXPLANATION OF PLATES

The photographs in plates XLVII and XLVIII were made with a Zeiss photomicrographic camera. Part of the photographs were taken with a No. A_2 objective and the remaining with the No. A_3 objective, having magnifications of × 10 and × 15 respectively.

PLATE XLVII

Fig. 1. Malva parviflora, Arizona, *Thornber 459*. × 10.

Fig. 2. Malva parviflora, Mexico, *Palmer 48*. U. S. Nat. Herb. No. 11767. × 10.

Fig. 3. Malva borealis, Sarepta, Russia. U. S. Nat. Herb. No. 11732. × 10.

Fig. 4. Malva parviflora, La Paz, Peru, *Buchtien 15*. U. S. Nat. Herb. No. 534457. × 10.

Fig. 5. Malva parviflora, Arizona, *Toumey 79*. U. S. Nat. Herb. No. 212556. × 10.

Fig. 6. Malva borealis, Great Britian. U. S. Nat. Herb. No. 813202. × 10.

Fig. 7. Malva borealis, Leeds, N. D. From a specimen in Gray Herbarium. × 10.

Fig. 8. Malva parviflora, Laramie, Wyo., *E. Nelson 2040*. × 15.

Fig. 9. Malva parviflora, Leeds, N. D. From a specimen in Gray Herbarium. × 15.

PLATE XLVIII

Fig. 10. Malva borealis, Limestone, Wyo., *A. Nelson 9532*. × 10.

Fig. 11. Malva borealis, Konigsberg. Field Museum No. 55533. × 10.

Fig. 12. Malva borealis, Herb. Flora Ingricae. Field Museum No. 54392. × 10.

Fig. 13. Malva borealis, San Bernardino, Cal., *S. B. Parish 2057*. × 10.

Fig. 14. Malva borealis, Europe, exact locality not given. × 10.

Fig. 15. Malva parviflora. U. S. Nat. Herb. No. 11743. × 10.

Fig. 16. Malva borealis, Copenhagen, Denmark. × 10.

Fig. 17. Malva rotundifolia, Milton, Ore. Univ. of Wyoming, No. 33701. × 10.

Fig. 18. Malva rotundifolia, Afghanistan. × 15.

Fig. 18. Malva rotundifolia, France. × 15.

Fig. 20. Malva rotundifolia, Colorado. × 15.

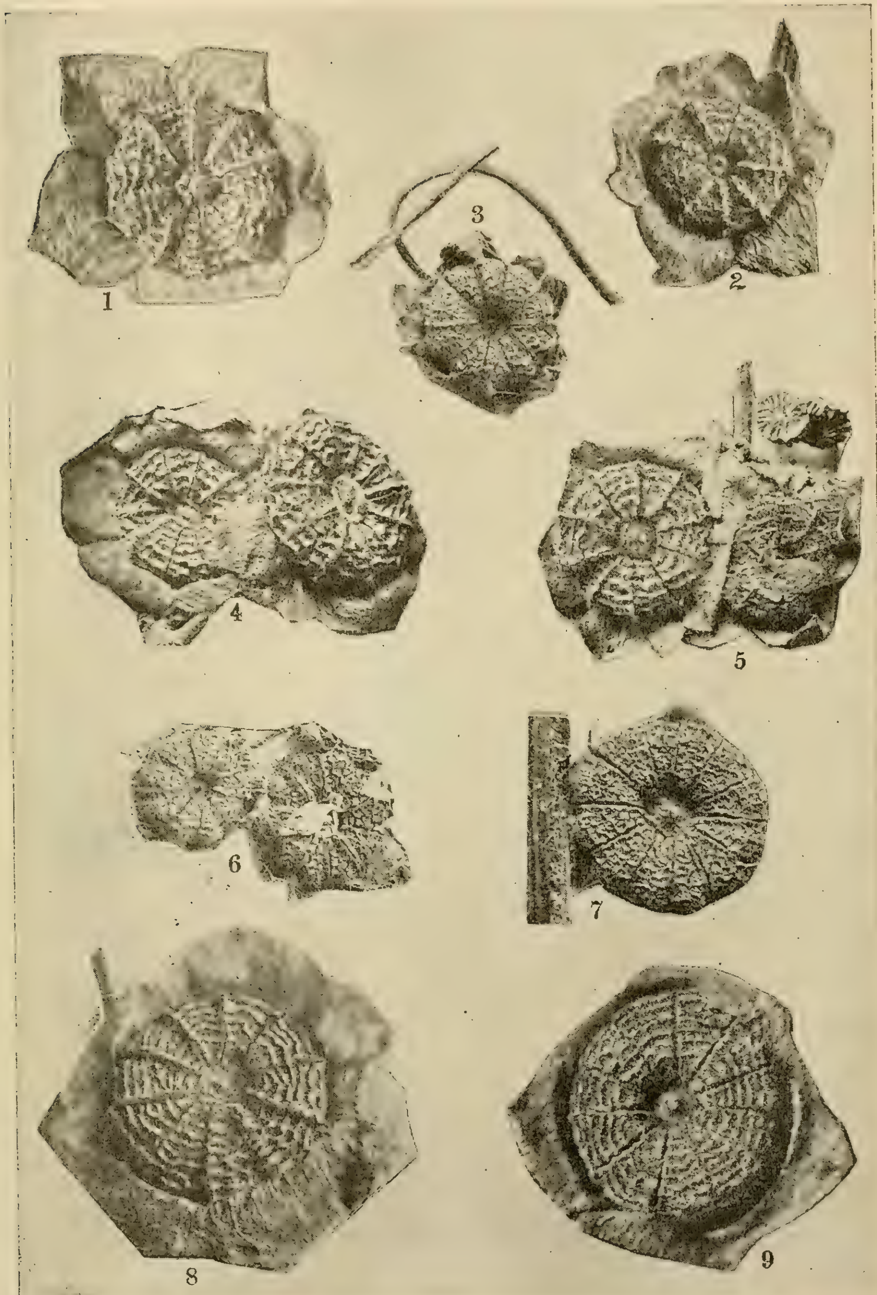

PLATE XLVII

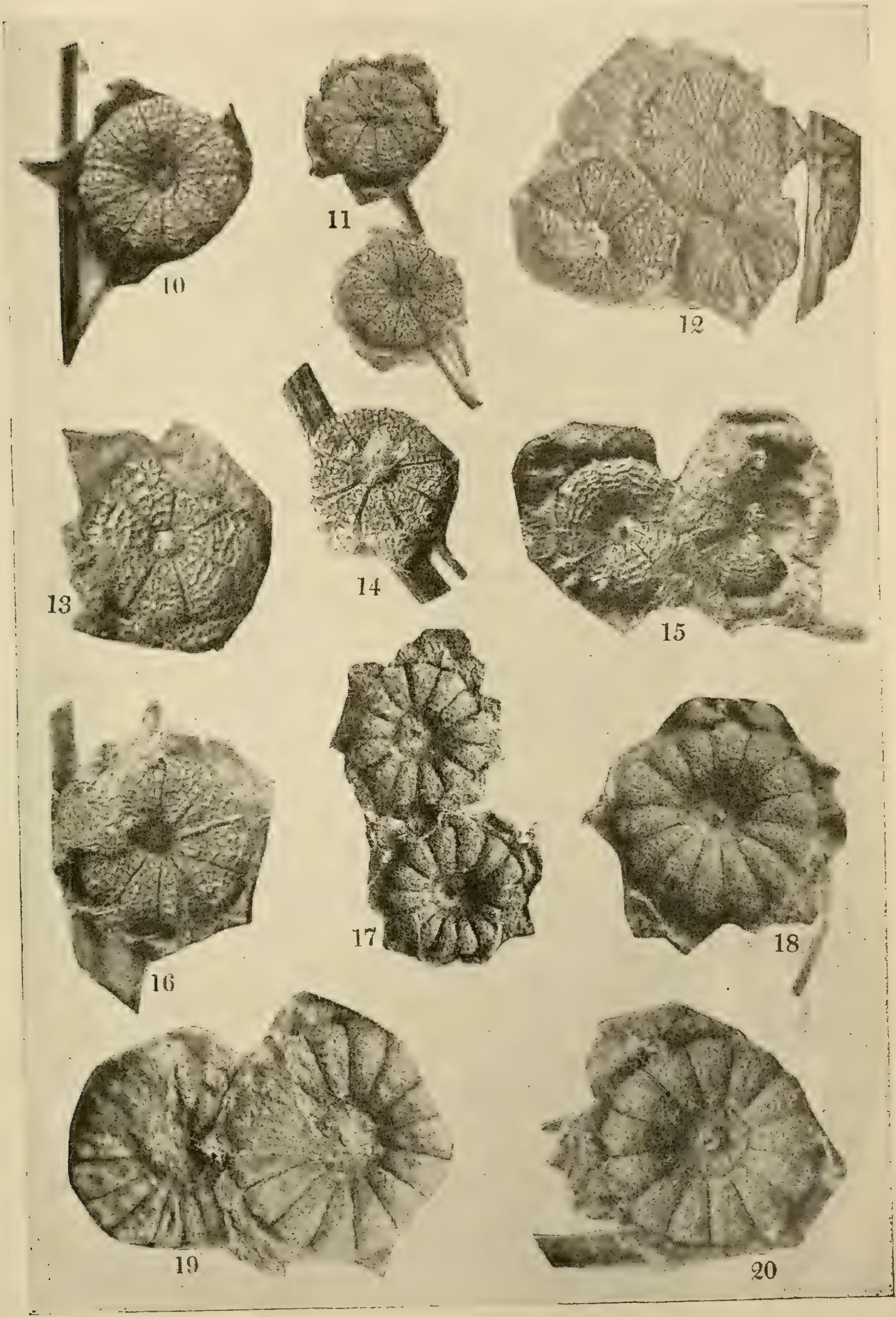

PLATE XLVIII

OBSERVATIONS ON BETULA IN MINNESOTA WITH SPECIAL REFERENCE TO SOME NATURAL HYBRIDS

C. O. Rosendahl

In 1904, Britton described a new species of birch from Minnesota[1] naming it *Betula Sandbergi* in honor of the collector, J. H. Sandberg, who found it growing in "Swamps in Hennepin County." The original description contained no information as to whether the new species was a tree or a shrub, nor did it state anything about the nature and color of the bark, probably because adequate data concerning these facts did not accompany the original collection.

In the 1907 edition of Britton's *Manual,* the species was inserted in the appendix and numbered 4a, which referred it to a position in the main text next to *Betula nigra.* It would appear, therefore, that its nearest affinity was assumed to be with the latter species. There seems to be no other reason for this alignment than that the specimens sent out by Sandberg, as indicated by the collection in the Herbarium of the University of Minnesota at least, were labeled *Betula nigra,* for the new species does not resemble the river birch in any of the determining and essential characters. The distribution was given as "Minnesota and Saskatchewan."

In 1909 B. T. Butler, in a paper on the Western American Birches,[2] described *B. Sandbergi* as a "shrub or shrub-like tree with dark brown bark, not separable into layers," and extended the range of the species to Montana.

From the time of the original collection in 1890 until the autumn of 1911 the species had apparently been entirely overlooked by collectors in Minnesota, for no other birch specimens in the entire Uni-

[1] Britton, N. L., Four New North American Birches, *Bull. Torr. Bot. Club,* 21:166. 1904.

[2] Butler, Bertram T., The Western North American Birches, *Bull. Torr. Bot. Club,* 36:421-440. 1909.

versity collection, except one by Sandberg, could possibly be referred to Britton's species. Considering the fact that Hennepin County, in which the birch had been first collected, has been more thoroughly studied than any other in the state, it seemed remarkable that a species, apparently so well marked, could have escaped notice completely for so long a time. A systematic attempt was therefore made to rediscover the plant, not, however, with much hope of early success, for it seemed that if at all common, it surely would have been encountered during the long intervening period. Furthermore, the indefinite legend, "Swamps, Hennepin County," which characterized Sandberg's collection, furnished no helpful clue, for Hennepin County is a part of Minnesota which is literally dotted with swamps. However, on a field trip early in September, 1911, a birch was found in a swamp near the middle of Hennepin County, which at once proved to be different from any of the common and well-known species of the state. It happened to be in excellent fruiting condition and ample material was secured.

One thing about the new material was, however, disconcerting. It did not resemble very closely Sandberg's collection in the University Herbarium, which some time subsequent to 1904 had been designated "Cotype" and was therefore taken to be authoritative. On the other hand, it seemed to agree admirably with Britton's description. Obviously there was a discrepancy of some kind and it seemed that the quickest way to straighten out the difficulty would be to compare both Sandberg's specimen and the recent collection with the type material. The two collections were accordingly sent to the New York Botanic Garden where Dr. Rydberg kindly made the comparison. The new material was stated to be "almost identical with the type specimen of *B. Sandbergi* except that the latter is a little more pubescent" and further that "there is no difference in the bracts of the catkins nor in the winged fruits. The mounted specimen collected by Sandberg differs only in the broader leaves and the thicker catkin, but those catkins are not broader than the catkins of some specimens collected by Mr. Butler in Montana and referred to *B. Sandbergi* by him."

The authenticity of the new collection was therefore fully enough established. About the Sandberg specimen there might be some slight doubt, although the larger size of the catkins and the greater width of leaf are insufficient to warrant separating it from the other.

During the spring following the rediscovery of *B. Sandbergi*

in Minnesota, efforts were made to secure staminate catkins and young twigs and also if possible to find more stations for the species. Several additional bushes were located, scattered throughout the tamarack swamp in which the shrub was found the previous season. Among these was one which differed from all the others in a very noticeable wintergreen flavor of the inner bark of the twigs and young branches, in which character it agreed with *Betula lutea.* The habit of the shrub, the small staminate catkins, and the appearance of the unfolding leaves, as far as it was possible to judge, resembled *Betula Sandbergi* somewhat closely. The unmistakable wintergreen flavor of the inner bark, however, aroused suspicion, and so the shrub was marked with the object of obtaining mature fruits and leaves later in the season. Two collections were made during the summer, one on July 11 and the other on September 22. From the July collection it was very clear that the shrub was not *B. Sandbergi,* for the catkins and bracts were even then much larger than the corresponding structures in mature specimens of the latter. Moreover, both bracts and nutlets were of a different shape and approached more closely those of *B. lutea.* That the shrub might be a depauperate individual of *B. lutea* suggested itself, but the size, form, serration and texture of the mature leaves at once precluded this possibility. Apparently, therefore, another unrecognized shrubby birch had been discovered.

Before venturing to describe it as a new species, however, further search in the field in the same general region, as well as in other localities in the eastern part of the state, was continued for two seasons. It seemed that if the plant merited specific recognition there ought to be more than a single individual found in a region where much collecting has been done. Summer before last another shrub of the same type was found in the vicinity of the first collection, and still another was discovered in one of the adjoining counties in a swamp about twenty-five miles towards the northeast.

A study of the catkins, bracts, nutlets and leaves of both *Betula Sandbergi* and the undescribed form revealed the interesting fact that the former occupies a place intermediate between *Betula papyrifera* and *B. pumila* or rather *B. pumila* var. *glandulifera,* (which is the form of the low birch which abounds in Minnesota), while the latter appears to be intermediate between *Betula lutea* and *B. pumila* var. *glandulifera.* It was therefore natural to conclude that

both of these interesting birches might be natural hybrids between the common and well-marked species of the region.

The fact that a number of birch species hybridize more or less freely in nature and under cultivation, has been observed for a long time, and several such hybrids have been described at different times. On the grounds of possibility, therefore, there was no reason why these forms might not be hybrids. But even though they might suggest through their intermediate characters that they were hybrids, still to make a mere categorical assertion to that effect without any additional evidence, seemed somewhat unjustifiable.

Several attempts to grow the seeds of both the hybrids have been made, but up to the present only three seedlings from the last sowing of *B. Sandbergi* have been obtained. These are yet too young and small to offer any proof one way or the other so that the hope of learning something through the segregation of parent strains in the second generation has not been realized. Another evidence of hybridity or of hybrid contamination in plant species has been strongly emphasized in recent publications of Jeffrey.[3] He has found in his investigation of a large number of known hybrids that the pollen always shows a large per cent of defective grains, and further that in many families where crossings readily take place, numerous forms occur whose parentage is not known, or is obscure, but which have defective pollen grains and thus indicate hybridity.

The pollen test was applied to all the birches involved in the suspected crossings and the facts revealed are quite significant. It was found that the pollen grains of the three common birches growing in the vicinity of the hybrids, namely *Betula papyrifera, B. lutea* and *B. pumila var. glandulifera,* ran nearly 100 per cent good on all the counts. This may readily be verified by an examination of the photo-micrographs (Plate XLIX). On the other hand, the pollen in the two suspected hybrid forms proved to have 25 to 40 per cent defective grains. If, therefore, defective pollen in considerable quantity is a reliable criterion of hybridity in plants, and Jeffrey's extensive observations along this line appear to have established it as a fact, then the assumption that the two birches in question are natural hybrids is amply sustained.

The intermediate character of the hybrids is made tolerably

[3] Jeffrey, E. C., Some Fundamental Morphological Objections to the Mutation Theory of De Vries. *American Naturalist,* 49:5. 1915.
Spore Conditions in Hybrids and the Mutation Hypothesis of De Vries. *Botanical Gazette,* 58:322. 1914.

clear from the two text figures, which are reproduced from camera lucida drawings, but a number of points need further elucidation.

As already stated, the only three well recognized species of birch which occur in the vicinity of these hybrids are *B. papyrifera, B. lutea,* and *B. pumila* var. *glandulifera.* The river birch, *B. nigra,* although found in Minnesota, is out of the question as a possible parent, for it does not occur within 45 or 50 miles of the tamarack swamps where the hybrids have been found.

Fig. 1. a-b Betula papyrifera; c-d-e B. papyrifera x pumila var. glandulifera; f-g forma maxima; h-i B. pumila var. glandulifera; k-l B. lutea; m-s B. lutea x pumila var. glandulifera.

In the case of *B. Sandbergi,* it seems quite clear that *B. papyrifera* is one of the parent species because of the very close resemblance the winged nutlets of the two bear to one another. In both, the wing is perceptibly wider than the nutlet and projects considerably above the base of the styles. The leaves resemble those of *B. pumila* var. *glandulifera* in size, form, serration and texture more than they do *B. papyrifera.* In the former the number of pairs of veins averages 6 to 7, in the latter 3 to 4, while the average for *B. Sandbergi* is 5. The shrub varies from 3 to 6.5 m. in height, with stems 3 to 7 cm. in diameter, and has a reddish or grayish brown

bark which does not peel into thin papery layers. There is no trace of wintergreen flavor in the inner bark of either *B. papyrifera* or *B. pumila* nor is there any in the hybrid *B. Sandbergi.*

In the latest monographic work on the Betulaceae,[4] Winkler describes among other hybrids one between *Betula papyrifera* and *B. pumila* raised by Zabel in the Münden Forstgarten from "American Seeds" and first described by the latter in "Mitteil. der Deutsche Dendrol. Gessell." 1895. This latter work is unfortunately not at my disposal, and Winkler's description does not distinguish the form sufficiently for me to assert whether or not it is identical with the one that is found growing in Minnesota.

That the *B. papyrifera* x *pumila* hybrid has been known to European botanists and gardeners for a much longer time but under another name, is asserted by Schneider,[5] who refers it to Aiton's *Betula excelsa* first described in "Hortus Kewensis" (3:337, 1789). This is contrary to the opinion expressed by Winkler, who regards *B. excelsa* as a garden form of *B. pubescens* (Regel before him regarded it as a sub-species of *B. alba)* but makes the statement that its place of origin is unknown.

From an examination of *B. excelsa* material from Breslau and the Botanic Garden of Petrograd, kindly loaned by the Arnold Arboretum, we feel certain that it is not identical with or even near to the *B. papyrifera* x *pumila* hybrid as it occurs in Minnesota.

The leaves of *B. excelsa* have a very characteristic rhombic-ovate to ovate-cordate form and vary at the base from broadly cuneate to faintly cordate. If a line is drawn across the widest part of the leaf, it cuts off an upper portion which is almost always an equilateral triangle, with the two legs hardly cutting into the serrations, and forming two-thirds the length of the leaf. The serrations are coarse and irregular.

The leaves of the Minnesota hybrid are rhombic-ovate to obovate, either rounded at the base or more often distinctly cuneate, rounded or slightly acute at the apex and evenly though often somewhat coarsely serrate. The widest part of the leaf is at or near the middle. The catkin, bractlet and samara of *B. excelsa* all resemble much more closely the corresponding structures of the *Betula pubescens-verrucosa-populifolia* group than they do our hybrid. In addition to this, *Betula excelsa* is said to be a densely branched,

[4] Winkler, Hubert, Betulaceae, *Das Pflanzenreich*, IV, 61:94. 1904.
[5] Schneider, C. K., Illustriertes Handbuch der Laubholzkunde.1, 108-109. 1906.

pyramidal tree, lending itself admirably to isolated planting for ornamental purposes, whereas *B. Sandbergi* is a shrub with 4 to 8 ascending stems which occasionally attain the aspect of straggling trees. It would be difficult to imagine how a pyramidal tree could arise from parents like *B. papyrifera* and *B. pumila.* The former has a habit of sending up mostly from a common root 2 to 4 stems which grow in a spreading manner, each forming an irregular

Fig. 2. a-d Betula papyrifera; e-f B. pumila var. glandulifera; g-h B. papyrifera x pumila var. glandulifera; k-l forma maxima; m-r B. lutea x pumila var. glandulifera; s-t B. lutea.

crown which is widest near the top. When only one stem is present it is never strictly erect or regular. *Betula pumila* is a typical shrub with ascending stems and branches.

All these facts contradict Schneider's assertion as to the origin and identity of *Betula excelsa,* and it seems more likely that Winkler is correct in assuming it to be a garden form of *B. pubescens.*

In the case of the hybrid between *B. lutea* and *B. pumila* var. *glandulifera,* a somewhat similar intermediate position is shown in

a number of characters. The catkins are somewhat smaller than in *B. lutea.* The lateral lobes of the bracts are slightly spreading, whereas in *B. lutea* they are erect. The leaves are considerably smaller than in the yellow birch. They have the texture of *B. pumila* var. *glandulifera* and average six pairs of veins to four and nine for *B. pumila* and *B. lutea* respectively. The samara is almost identical with that of *B. lutea* which is characterized by having the wing narrower than the body of the nutlet and not projecting above the base of the styles (Fig. 2, n,p,r,t.). In both these respects it is strikingly different from the fruit of both *B. papyrifera* and *B. Sandbergi.* The flavor of wintergreen in the bark of the hybrid is an unmistakable evidence of its connection with *B. lutea* and is, in the opinion of the writer, the character of most significance. From these facts there can be no doubt that *B. lutea* is one of the parents of this hybrid, but the parentage on the other side is less easy to establish.

As already stated, only three species of birch in addition to the hybrid *B. Sandbergi* occur in the part of the state where this new hybrid has been observed. They are found pretty well intermixed. The crossing must therefore be between *B. lutea* and one of the three other forms. From the evidence so far deducible which of these appears the most likely?

A cross between *B. lutea* and *B. papyrifera* would probably give rise to a tree instead of a shrub, for in this region both of these species are good-sized trees. The leaf would be expected to resemble either one or the other of the parents or be intermediate between them. In no respects does it comply with these expectations, for as figure 1 (m,n,p,q,s) shows, it is quite distinct both in form and size, and the texture is also different. The catkin, bract, and samara as already shown resemble *B. lutea* very closely and indicate no admixture of *B. papyrifera.* That *B. Sandbergi* might be one of the parents is not impossible, yet it appears rather doubtful, for the reason that in one of the places where the shrub was found, only *B. lutea, B. pumila* var. *glandulifera* and *B. papyrifera* occurred. Furthermore, the spontaneous crossing between a species and a somewhat rare hybrid seems less likely to take place than between good and abundant species. On the whole, therefore, it appears that *B. pumila* var. *glandulifera* must be the other parent. This species is abundant in the swamps where the hybrid has been found and as there is nothing in the form and appearance of its catkin,

bract, samara and leaf to disprove this assumption, it seems justifiable enough. However, the question can not be said to be settled until actual crossing has been carried out under control.

Winkler, in the preparation of the above-mentioned monograph, had under observation some specimens loaned him by Schneider and Zabel, one of which he surmises to be a cross between *B. lutea* and *B. pumila.* Apparently he felt that the material was insufficient or that there were not conclusive data enough at hand, otherwise it seems he would have described it and included it among the rest of the hybrids diagnosed.

Two years later, however, Schneider[6] described such a hybrid and stated it to have been obtained from Michigan by Purpus of Darmstadt, the latter's brother having sent it to him from Clark's Lake. It is named *B. Purpusi* and is described as a shrubby plant of the *pumila* form and is further characterized as var. *typica,* to distinguish it from a tree-like plant growing in the Darmstadt garden, apparently raised from seed from the Michigan plant by Purpus. This Darmstadt plant is designated var. *luteoides.*

Whether or not these forms are identical with the Minnesota material, only actual comparisons of specimens can show, for descriptions alone are not adequate in such cases. Unfortunately, on account of the present European upheaval, the exchange of material is out of the question, and it must remain for the future to settle these points.

A hybrid between *B. lenta* and *B. pumila* has also been known for some time, being described by Jack in *Garden and Forest* in 1895. This plant was grown in the Arnold Arboretum and bears a close general resemblance to the *B. lutea* x *pumila* var. *glandulifera* hybrid, as would naturally be expected. The characters of fruiting catkin, bract and samara are sufficiently distinct, however, to separate them without any difficulty.

Since none of these hybrids seem to have been observed in the field to any extent outside of Minnesota, possibly because they may be more or less easily confused with young specimens of one or the other of the parent species, it seems desirable to add to what has already been said, an analytical key to all the hybrids and the parent species, and in addition brief diagnostic descriptions of the former.

[6] Illustriertes Handbuch der Laubholzkunde. 1, 102-103.

Analytical Key to Species and Hybrids

I. Leaves 6-10 cm. long, mostly thin and papery, 6-12 pairs of veins; fruiting catkins 3 cm. long or more; trees

a. Fruiting catkins sessile or nearly so, erect, oblong-ovoid 11-18 mm. thick; wing narrower than nutlet; leaves with 9-12 pairs of veins, inner bark with wintergreen flavor.

m. Leaves oblong-ovate or ovate, sharply and evenly serrate; bract smooth and firm; bark not peeling — *B. lenta*

n. Leaves ovate, mostly oblique at base, sharply doubly-serrate; bract ciliate-pubescent along the margins, thinnish; bark peeling — *B. lutea*

b. Fruiting catkins pedicelled, spreading or pendent, 8-10 mm. thick, wing wider than nutlet; leaves with 6-9 pairs of veins, inner bark without wintergreen flavor — *B. papyrifera*

II. Leaves 2-6 cm. long, thick and firm in texture, 3-7 pairs of veins; fruiting catkins mostly less than 3 cm. long; shrubs

a. Leaves ovate to broadly ovate or oval, 5-7 pairs of veins; fruiting catkins oblong-ovoid, 1.5-2.8 cm. long, 10-13 mm. thick, short-stalked or sessile; bracts 5.5-7 mm. long; twigs aromatic

m. Bracts about as broad as long, smooth or nearly so, samara obcordate, about 4 mm. broad — *B. lenta* x *pumila*

n. Bracts longer than broad, lobes ciliate-pubescent along the margins, samara obovate, about 3.4 mm. broad — *B. lutea* x *pumila* var. *glandulifera*

b. Leaves rhombic-ovate, obovate or oval, 3-5 pairs of veins; fruiting catkins cylindric or ovoid-cylindric, 5-7 mm. thick, distinctly pedicelled; bracts 3-5.5 mm. long; twigs not aromatic

m. Leaves rhombic-ovate or obovate; fruiting catkins 2-3 cm. long, 6-7 mm. thick; bracts 4-5.5 mm. long; wing as wide or wider than nutlet; tall shrub — *B. papyrifera* x *pumila* var. *glandulifera*

n. Leaves obovate to oval; fruiting catkins 1-2.8 cm. long, 5-6 mm. thick; bracts 3-3.5 mm. long; wing of samara narrower than nutlet, low or medium sized shrub — *B. pumila* var. *glandulifera*

Note: *B. lenta* and the hybrid *B. lenta* x *pumila* are included in the key, together with descriptions for the purpose of comparison. The writer is not aware that the latter has been found in any locality outside the Arnold Arboretum, and although *B. lenta* has been reported from Minnesota, it is extremely doubtful whether it occurs in the state.

It is not necessary here to describe the first three species, for they are quite common throughout their range, easily recognized and generally well known. Some facts about their distribution in the middle northwest are worth noting.

Betula lenta L. is reported to range as far west as northern Ontario and central Iowa. From this one would expect it to occur within the borders of Minnesota, and in fact several specimens labelled *B. lenta* have been collected in different parts of the state. None of these proves upon careful examination to be correctly determined. One of these, by W. A. Wheeler (No. 1651) from southeastern Houston County, has leaves which in outline resemble very closely typical *B. lenta* leaves, but the serrations are too coarse and uneven, and the bracts are conspicuously ciliate-pubescent along the margins. The specimen can therefore be referred to *B. lutea* without any doubt whatever. There is nothing in the present topography nor anything of the nature of geologic barriers to prevent *B. lenta* from occurring in Minnesota if the report of its two western outposts given in standard manuals and floras is correct. We are therefore constrained to regard its occurrence in northwestern Ontario as doubtful.

Betula lutea Michx. occurs as a tree of varying height, reaching its greatest size on the wooded slopes and side gullies of the St. Croix and Mississippi River valleys, where it usually grows to a height of 50 to 70 feet and a trunk diameter of 12 to 18 inches. It is found short distances up some of the valleys of the western tributaries of the Mississippi from the southern border of the state to the Minnesota River, and is also common in the tamarack swamps of the east central and northeastern parts of the state. In these localities it is smaller and is more irregular and spreading.

A few puzzling forms of this species occur, some with the fruiting catkins much reduced in size, others with thick, leathery leaves. Possibly these are other hybrids or Mendelian segregates. At present material is insufficient and not enough observations have been made in the field to warrant any disposition of them.

Betula papyrifera Marsh. is common throughout the wooded areas of the state and is quite variable in general appearance as well as in foliage and fruit.

On the north shore of Lake Superior *B. papyrifera* var. *cordifolia* Regel. is common and attains great size. In fact, some of the

largest birch trees noted in the state by the writer, occur here and are mainly this variety. They differ from the ordinary forms of the species, as it occurs in other parts of the state, by the more yellowish tinge of the papery bark and more erect and solitary habit of growth. The ripe catkins attain a length of 5 to 6 cm. and a diameter of 10 to 11 mm.; the nutlet is usually about 0.5 mm. longer than the average of *B. papyrifera* while the styles are mostly twice as long or about 2 mm. In the original description Regel cites a specimen from Pic River, Lake Superior, which compares very closely in catkin and nutlet characters with specimens from near Grand Marais, but in which the leaves average somewhat smaller and are a little more narrowly cordate.

In the Grand Marais region the large trees are scattered abundantly through the forest on the slopes.

In addition to this variety, the most noteworthy form is one collection from near the middle of Hennepin County (Rosendahl 2506) in which the lateral lobes of the bracts are very short and ascending or almost obsolete, and the middle lobe narrow and sharp-pointed. The leaves are narrower than normal and long-acuminate. Another form represented by two collections, one from Hennepin County (Rosendahl 2690) and one from Dent, Otter Tail County (Bergman 2858) has rhombic-ovate leaves, cuneate at the base and abruptly narrowed and acuminate at the apex, and slender petioles 2 to 3 cm. long. In still other specimens from the west central part of the state (notably Frost No. 3631) the leaves are broadly ovate or nearly orbicular.

It is possible, in fact highly probable, that some of these variations are the breeding out or segregation products of former crosses between *B. papyrifera* and other species of birch of the particular regions.

Betula papyrifera x pumila var. glandulifera

B. Sandbergi Britton. Bull. Torr. Bot. Club. 31:166. 1904.

A shrub or sometimes a shrub-like tree 2-10 m. high; bark dark brown, not separating into layers; young branches rusty-pubescent, in late summer or fall mostly shedding the hairs and remaining merely puberulent and showing scattered resiniferous dots and lenticels, 1-3 year old twigs gray-glaucous, the epidermis of which splits and reveals the reddish-brown color of the perma-

nent bark of older twigs and branches; leaves with 4-5 pairs of veins, rhombic-ovate to obovate, cuneate or sometimes rounded at the base, broadly acuminate or rounded at the apex, 2.5-5.5 cm. long, 1.5-3.5 cm. wide, (on sterile shoots usually more broadly ovate and larger, 5-7 cm. long, 4-5 cm. wide, dentate and more pubescent throughout), serrate, the serrations somewhat crenate and occasionally uneven, pubescent beneath, especially along the veins, at length becoming nearly or quite glabrous, dotted with fine resinous glands, dull green above, lighter beneath, thick and firm in texture, finely reticulate-veined, the reticulations conspicuous on the upper surface in dried specimens; petioles 7-13 mm. long; staminate catkins borne singly or in pairs at the ends of the branches, 3-5 cm. long, 5 mm. thick; pistillate catkins 10-14 mm. long, 1.5-2 mm. thick, pedicelled, bearing 1-2 leaf-like bracts; fruiting catkins cylindrical, erect, 2-2.5 cm. long, 6-7 mm. in diameter, pedicel about 1 cm. long, bracts 4 mm. long, about 3.6 mm. wide, lateral lobes spreading, shorter than the tapering middle lobe, puberulent on the back and finely ciliate-pubescent along the margins of the lobes; samara 3.2-3.5 mm. wide, nutlet 1.3 mm. wide, mostly slightly narrower than the wing. (Fig. 1, c-e, fig. 2, g-h.)

Infrequent in tamarack swamps. Has been found in four different swamps of Hennepin County, in each case associated with the parent species. Also reported from Saskatchewan and Montana. To what extent if any the hybrid breeds true, it is impossible to say, but most of the plants so far found are quite uniform in size, mode of branching and growth, color of bark, texture of leaves, fruiting catkins, etc. They may all, however, be hybrids of the F_1 generation since they occur where the parent species abound. One notable exception has been observed which may conveniently be designated and described as:

Forma **maxima.** Very large spreading shrub or small tree, with 3-4 irregularly branching stems from a common root, 8-10 m. high, 12-17 cm. in diameter; bark gray, peeling slightly into thin layers, young twigs glabrous, branches slender and somewhat pendulous; leaves rhombic-ovate to obovate, distinctly cuneate at the base, acute or rounded at the apex, 3.5-6.5 cm. long, 1.5-4.5 cm. wide, mostly coarsely serrate to dentate, glabrous or with only a few scattered hairs along the veins, finely reticulate-veined; petioles 12-17 mm. long; fruiting catkins 2.5-3.6 cm. long, 7-9 mm.

thick; bracts 5-6 mm. long, 3-5 mm. wide; samara 3.3 mm. wide, nutlet slightly wider than the wing. (Fig. 1, f-g, fig. 2, k-l.)

We are inclined to regard this form as belonging to the F_2 generation standing much closer to the *B. papyrifera* parent than the ordinary hybrid, in its larger size, the character of the bark, the coarseness of leaf serrations, and the size of the fruiting catkins and the length of their pedicels.

Only two trees of this variety have been found, both growing in a small tamarack swamp near the center of Hennepin County (Rosendahl Nos. 2685, 2686, 2731, 2732).

Betula lutea x **pumila** var. **glandulifera** n. hybr.

A shrub or shrub-like tree 3 to 6 m. high with grayish-brown bark, not separating into layers, inner bark with wintergreen flavor; young twigs puberulent or thinly pubescent, with a few small resin glands, 1-3 year old twigs gray-glaucous, changing to grayish-brown on older branches; spur shoots numerous with closely crowded leaf scars; leaves ovate to obovate, with 5-7 pairs of veins, slightly cordate to broadly cuneate at the base, acuminate at the apex, 2.5-6 cm. long, 1.5-3.5 cm. wide, dull green and glabrous above, much lighter and at first pubescent along the veins beneath, soon becoming nearly or quite glabrous, often glandular-dotted, mostly unevenly and sharply serrate to crenate-serrate, thick and firm in texture; petioles stout, 7-14 mm. long with a few scattered hairs; staminate catkins borne singly or in pairs at the ends of the branches, 3-5 cm. long in anthesis, about 5 mm. in diameter; pistillate catkins erect, sessile or nearly so, about 10 mm. long, 2-2.3 mm. thick; fruiting catkins oblong ovoid, 1.5-2.8 cm. long, 10-12 mm. in diameter, erect, pedicel 3-8 mm. long; bract 5.4-7 mm. long, 4.3-5.5 mm. wide, ciliate-pubescent along the margins of the lobes, lateral lobes broad and only slightly spreading, middle lobe blunt triangular; samara ovate to slightly obovate, 2.5-3 mm. wide, nutlet 1.6-1.8 mm. wide, about twice as wide as the wing. (Fig. 1, r-s, fig. 2, m-r.)

In tamarack swamps, comparatively rare. Only three collections from Hennepin County and one from Anoka County have thus far been seen. (The plant referred to by Schneider and collected at Clark's Lake, Michigan, may perhaps be identical with ours.)

This hybrid differs from *B. Sandbergi* in the more regularly ovate leaves with less cuneate base, larger number of lateral veins, stouter and more nearly sessile fruiting catkins, larger fruiting bracts and the narrowly winged samaras. In addition, the wintergreen flavor of the bark is very characteristic.

As in the other hybrid, forms occur which resemble one or the other of the parent species more closely. One such collection (Rosendahl 2820) approaches *B. lutea* in the form, texture and serration of the leaves, but their size averages much less—2.5-5.5 cm. long, 1.4-3.2 cm. wide—and the fruiting catkins are uniformly pedicelled. (This may possibly be identified with Schneider's *B. Purpusi* var. *luteoides,* see l. c., p. 102-107.)

Whether it belongs to the F_1 or the F_2 generation, it is difficult to say, but we are inclined to regard it as a second generation hybrid. An examination of its pollen showed nearly 40 per cent defective grains, so there can be little doubt about its hybrid nature.

Betula pumila x **lenta** Jack, Garden and Forest, 8: 243. 1895.

Betula Jackii Schneider, Lehrb. der Laubholzk. 107. 1906.

Shrub or small tree with brownish-red bark; young twigs densely pubescent, becoming glabrous or nearly so towards the end of the season, not glandular-dotted, older twigs brownish-red with conspicuous lenticels; inner bark with wintergreen flavor; leaves with 5-7 pairs of veins, ovate, rounded at the base, acuminate at the apex, 2.5-5 cm. long, 1.5-3.5 cm. wide, mostly sharply and unevenly serrate, thinly pubescent above, somewhat lighter and densely pubescent beneath, in age becoming nearly glabrous except in the axils of the veins beneath, thick and firm in texture; staminate catkins solitary or in two's, terminal or sometimes axillary, 4-5 cm. long in anthesis; pistillate catkins 10-15 mm. long, about 4 mm. in diameter; fruiting catkins ovoid-cylindric, 2-2.7 cm. long, 9-12 mm. in diameter, short-stalked or nearly sessile, bracts 5.7-7 mm. long, 5-6 mm. wide, at first slightly pubescent on the back and margins, but becoming glabrous in age, lateral lobes spreading, triangular-pointed, as large as the middle lobe; samaras obovate to obcordate, 3.2-3.4 mm. wide; nutlet 1.7-1.9 mm. wide, about twice as wide as the wing.

From the Arnold Arboretum, where it arose spontaneously near

a group of the parent plants. It resembles the hybrid between *B. lutea* and *B. pumila* var. *glandulifera* somewhat closely but can be distinguished by the more reddish bark of the branches, more pubescent young twigs and leaves, the absence of resin glands on the leaves and twigs, and by the nearly or quite glabrous bracts. The dense pubescence of the eastern hybrid and the lack of glands upon the herbage are to be ascribed to the fact that the young twigs and foliage of typical *B. pumila* of the east are mostly downy pubescent and not at all glandular.

Betula pumila var. **glandulifera** Regal Bull. Soc. Nat. Moscou. 38:41. 1865.

B. glandulifera (Regel) Butler, Bull. Torr. Bot. Club, 36. 1909.

The typical *B. pumila* of eastern North America does not appear to occur within the boundaries of Minnesota, although credited to the state in reports and manuals.

The form which is found nearly everywhere in our tamarack swamps and bogs from the southern to the northern boundaries of the state is the variety *glandulifera*. The young branches are always more or less glandular dotted, mostly puberulent and sometimes with a few scattered, long hairs, but never woolly pubescent as in the eastern representatives of the species. The foliage is nearly always glandular and glabrous throughout, or at most only thinly pubescent when young but soon becoming smooth all over. Sometimes a few scattered hairs remain on mature leaves towards the base and on the puberulent petioles. In form the leaves vary from broadly obovate to wedge-obovate, and are crenate-serrate to coarsely dentate. Some specimens from the Lake of the Woods and the northwestern corner of the state are more densely glandular-dotted on the young twigs than specimens from other parts of the state and seem to occupy an intermediate position between *B. pumila* var. *glandulifera* and *B. glandulosa*. There are, however, no collections of the latter species from Minnesota in the University Herbarium, and it is very doubtful if it reaches the state although it has been so reported.

EXPLANATION OF PLATE XLIX

Photo-micrographs of pollen from mature anthers, stained with acid fuchsin and mounted in lactic acid. All figures magnified about 200 times and photographed to the same scale.

Fig. 1. Betula papyrifera. Pollen practically all good.

Fig. 2. Betula Sandbergi (B. papyrifera x pumila var. glandulifera). Pollen with about 45 per cent defective grains.

Fig. 3. Betula pumila var. glandulifera. Pollen all good.

Fig. 4. Betula lutea. Pollen practically all good.

Fig. 5. Betula lutea x pumila var. glandulifera. Pollen with about 33 per cent defective grains.

Fig. 6. Betula lenta. Pollen all good.

Fig. 7. Betula Jackii (B. lenta x pumila). Pollen with about 25 per cent defective grains.

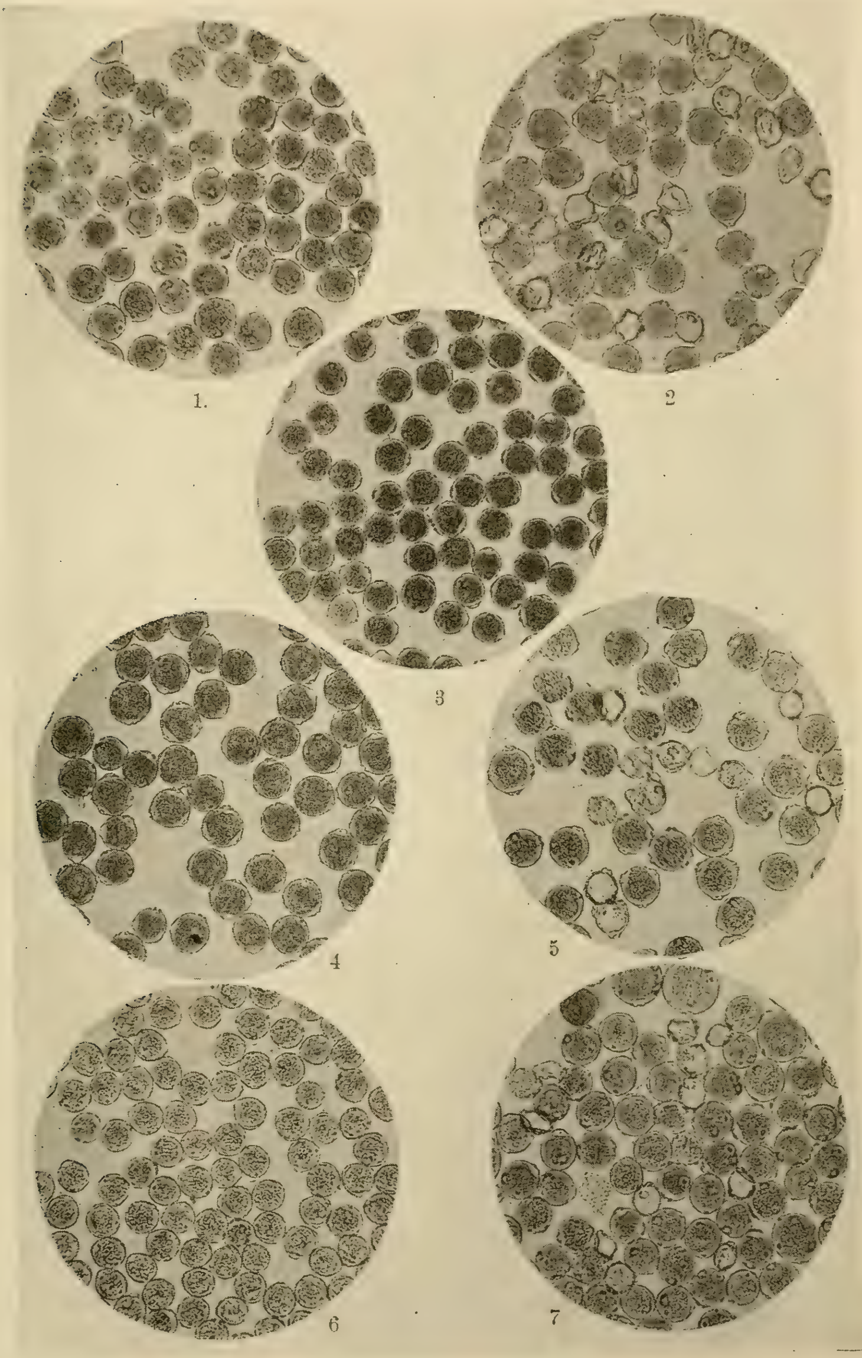

PLATE XLIX

REPUTED MINNESOTA PLANTS WHICH PROBABLY DO NOT OCCUR IN THE STATE

C. O. Rosendahl and F. K. Butters

Many of the reports of the occurrence of species of vascular plants in Minnesota are based upon the *Catalogue of Plants of Minnesota,* by I. A. Lapham, and upon the much more extensive *Catalogue of Minnesota Plants* published by Warren Upham in 1884. The pioneer work of Lapham, Winchell, Upham, and others, upon which the latter catalogue is based, deserves high praise, considering that it was often incidental to work along other lines of investigation and that much of it was done without adequate collections from the various parts of the state, and often without the opportunity of careful comparison with material from other parts of the country.

However, there are several considerable sources of error in this catalogue. There was a very evident tendency on the part of its author to accept without question reports or lists of plants emanating from amateur and semiprofessional botanists in different parts of the state. Species were frequently listed because they had been reported near the boundaries of Minnesota, and might therefore be expected to occur within the state. Furthermore, many specimens which were actually seen by the author were not critically determined and were reported under the names of allied species. In some of these cases the specimens are now in the Herbarium of the University of Minnesota and can be readily redetermined; but in many other cases, the original report is apparently based upon identifications made in the field, and one can only infer what plant was actually at hand.

Since the publication of Upham's Catalogue, a number of partial lists by various authors have appeared, some of them revisions

of limited groups of plants, others accounts of the flora of particular parts of the state. These lists have varied much in the critical character of the work and are therefore of quite unequal value. In view of these facts it is not surprising that the standard floras for the eastern part of North America, Gray's *Manual,* Britton's *Manual* and Britton and Brown's *Illustrated Flora,* contain many erroneous statements concerning the occurrence of species in Minnesota.

During the years since the appearance of Upham's *Catalogue,* a great amount of Minnesota material has accumulated in the Herbarium of the University of Minnesota, and it has become possible to check over the published lists and to correct many of the errors contained in them. As the time does not yet seem ripe for a complete Flora of the state, the authors of the present paper have deemed it advisable to publish a checking-out list of those plants which appear to have been erroneously reported in this state.

Naturally, the evidence varies much in different species. In the case of some of the plants reported by Upham, and of practically all of those included in later lists, the original specimens are at hand and have been re-examined. In other cases, although there is no direct evidence of the original collections, it appears from abundant herbarium material that certain species have been habitually misdetermined by collectors. In still other cases, the evidence is entirely negative,—merely the fact that in over thirty years of more or less continuous collecting in the state no specimen of the species in question has found its way into the Herbarium of the University. These last cases differ considerably in value for various reasons. Obviously a small and inconspicuous species of *Carex* might be overlooked by collectors more readily than some large *Cypripedium* or *Lilium.* The authors of this list have endeavored to make clear in each case the evidence upon which their report is based. As they recognize that this evidence is largely negative and therefore inconclusive, they will particularly welcome authentic reports of the occurrence of any of these species in the state of Minnesota; especially will they be pleased to receive information from any of the other herbaria of the country regarding the occurrence of any of these species either in this state, or in its immediate vicinity. In return they will always be glad to furnish other workers with reports of the occurrence or distribution of species in Minnesota, based upon the collections in this Herbarium.

The following, the first installment of such a checking-out list, covers the Pteridophytes, the Gymnosperms, and the Monocotyledons, and it is expected to publish similar lists of the Dicotyledons in forthcoming numbers of the *Minnesota Botanical Studies.*

Bibliographic list of principal publications from which the reports have been made and checked.

Lapham, I. A. Catalogue Pl. Minn., Rep. Minn. Hort. Soc., 1875.

Upham, Warren. Catalogue of the Flora of Minnesota. Geol. and Nat. Hist. Survey, Rep. XI, 1883; reprinted, 1884.

Arthur, J. C. Rep. Botan. Work in Minn. for 1886. Bul. 3, Geol. and Nat. Hist. Survey of Minn., 1887.

Upham, Warren. Suppl. Minn. Flora, Bul. 3, Geol. Nat. Hist. Surv., 1887.

Hill, E. J. Flora of St. Croix Region. Bot. Gazette, May 1891.

MacMillan, Conway. Metaspermae of the Minnesota Valley, Botanical Series I, Geological and Nat. Hist. Survey of Minn. 1892.

Holzinger, J. Determinations of plants collected by Dr. J. H. Sandberg in northern Minnesota during 1891. Minn. Bot. Studies, 1: 517. 1896.

Wheeler, W. A. Contributions to a knowledge of the Flora of Southern Minnesota. Minn. Bot. Studies, 2: 353. 1900.

————. Contributions to a knowledge of the Flora of the Red River Valley in Minnesota. Minn. Bot. Studies, 2: 569. 1901.

————. Catalog of Minnesota Grasses. Minn. Bot. Studies, 3: 83. 1903.

Lyon, H. L. Pteridophytes of Minnesota. Minn. Bot. Studies, 3: 245. 1903.

Rosendahl, C. O. An addition to the knowledge of the Flora of Southeastern Minnesota. Minn. Bot. Studies, 3: 257. 1903.

Sheldon, E. P. Some extensions of plant ranges. Minn. Bot. Studies, 1: 14. 1894.

————. Revised descriptions of Minnesota Astragali. Minn. Bot. Studies, 1: 54. 1894.

————. Further extensions of plant ranges, Minn. Bot. Studies, 1: 66. 1894.

————. Compilation of records of some Minnesota Flowering plants. Minn. Bot. Studies, 1: 223. 1895.

————. Additional extensions of plant ranges. Minn. Bot. Studies, 1: 583. 1896.

Ramaley, Francis. Revision of the Minnesota grasses of the tribe Hordeae. Minn. Bot. Studies, 1: 105. 1894.

Fox, H. G. On the genus Cypripedium with reference to Minnesota species. Minn. Bot. Studies, 1: 423. 1895.

Heller, E. E. Corrections and additions to the Flora of Minnesota. Minn. Bot. Studies, 2: 30. 1898.

Gray's New Manual of Botany, 7th ed. 1908.

Britton, N. L. Manual of the Flora of the Northern States and Canada, 1st ed. 1901.

Britton, N. L., & Brown, A. Illustrated Flora of the Northern States and Canada. 2nd ed. 1913.

In the following list, the statement *no specimens* indicates that in the collections of the herbarium of the University of Minnesota there are no specimens of the species in question, collected in Minnesota.

The statement *reports based on wrong determinations* indicates that specimens in the University Herbarium, bearing the label of the species in question prove to belong to other species.

The nomenclature employed is that used in the seventh edition of Gray's *Manual,* and the species are listed in the order in which they occur in that work.

Pteridophyta

Phegopteris Robertiana (Hoffm.) A. Br.
Reported from Minnesota by D. C. Eaton; no specimens.

Cheilanthes lanosa (Michx.) Watt.
Reported in Gray's *Manual* as occurring in Minnesota; no specimens.

Cryptogramma acrostichoides R. Br.
Inferred in Upham's *Catalogue* to occur in Minnesota; no specimens.

Polystichum acrostichoides (Michx.) Schott.
Reported in Upham's *Catalogue;* no specimens.

Polystichum Lonchitis (L.) Roth.
Reported in Upham's *Catalogue* and in Lyon's list of the Pteridophyta of Minnesota; the latter report is based on an incorrect determination of a specimen of *Nephrolepis* sp. which is labelled from the north shore of Lake Superior; whether this is a case of mixed labels, or the collection of a cultivated plant cannot be determined; no specimens.

Polystichum Braunii (Spenner) Fée.
Inferred in Upham's *Catalogue* to occur in Minnesota; no specimens.

Aspidium noveboracense (L.) Sw.
Reported in Britton & Brown's *Illustrated Flora;* no specimens either from Minnesota or the adjacent states; report probably based on incorrect determination of *A. thelypteris* (L.) Sw.

Aspidium marginale (L.) Sw.
Reported in Upham's *Catalogue;* no specimens; it probably does not occur.

Aspidium Bootii Tuckerm.
Reported in Upham's *Catalogue,* and implied in Britton & Brown's *Illustrated Flora;* no specimens.

Woodsia glabella R. Br.

Reported in Upham's *Catalogue;* report seems to be based on some incomplete specimens, which are certainly not this fern, and are probably *Cystopteris fragilis* (L) Bernh.

Woodsia scopulina D. C. Eaton.

Previous reports of this species should be referred to *W. Cathcartiana* Robinson, and to an incorrectly determined specimen of *W. oregana* D. C. Eaton.

Dicksonia punctilobula (Michx.) Gray.

Does not occur; report based on incorrect determinations.

Botrychium lanceolatum (Gmel.) Ångstrom.

Suspected by Upham to occur in northeastern Minnesota; no specimens.

Salvinia natans (L.) All.

The reports of the occurrence of this species in Minnesota are based on its spontaneous appearance at the University Greenhouse in a tub of water in which had been placed a quantity of aquatic plants, muck, etc., collected in Sweeney Twin Lakes in the vicinity of Minneapolis. From this origin it has flourished in the greenhouses of the University for more than thirty years. It has never been found growing in the open in Minnesota, though a careful search has been made in the Sweeney Twin Lakes and elsewhere. At the time when it appeared a number of aquatic plants from outside of the state were being handled in the greenhouse, and we are constrained to think that this plant was introduced along with some of them.

Equisetum litorale Kühlewein.

Reported in Gray's *Manual;* no specimens.

Equisetum hiemale L. var. *robustum* (A. Br.) A. A. Eaton.

Reported in Holzinger's list of Sandberg's Minnesota Plants; no specimens.

Lycopodium selago L.

Reported in Upham's *Catalogue* from the north shore of Lake Superior; no specimens.

Lycopodium sitchense Rupr.

Reported in Gray's *Manual* from the north shore of Lake Superior; no specimens.

Lycopodium sabinaefolium Willd.

Reported in Upham's *Catalogue* as frequent northward; probably confused with forms of *L. complanatum* L. as there are no Minnesota specimens of *L. sabinaefolium.*

Selaginella apus (L.) Spring.

In Upham's report this species is suspected to occur in the southern part of the state, and Britton and Brown give its range as "Northwest Territory"; up to the present it has not been collected.

Isoetes lacustris L.
Reported in Upham's *Catalogue* and Lyon's list of Pteridophyta of Minnesota; should be referred to *I. macrospora* Dur.

Gymnospermae

Picea rubra (Du Roi) Dietr.
Reported in Gray's *Manual* as occurring in Minnesota; no specimens; it is extremely doubtful if it occurs in the state.

Juniperus communis L.
The arborescent form does not occur in the state; the common form throughout is var. *depressa* Pursh.; var. *montana* Ait. grows on Isle Royale, and it is likely that it occurs on the north shore of Lake Superior.

Angiospermae

Monocotyledones

Typha angustifolia L.
Does not occur in the state; a single specimen in the University Herbarium, collected by J. H. Sandberg in Carleton County, is so labelled but is merely a small specimen of *T. latifolia* L.

Sparganium americanum Nutt.
Implied in Britton's *Manual* to occur; the only Minnesota specimens in the University collection are of the var. *androcladum* (Engelm.) Fernald and Eames.

Sparganium simplex Huds.
No specimens; the report of this species appears to be based on specimens of *S. diversifolium* Graebner and *S. diversifolium* var. *acaule* (Beeby) Fernald and Eames.

Potamogeton illinoensis Morong.
Reported by Sheldon, but confused with *P. angustifolius* Berchtold & Presl., and *P. americanus* C. & S. in the University collections, and it is doubtful whether it occurs.

Potamogeton foliosus Raf.
Reported in Upham's *Catalogue;* no specimens.

Potamogeton hybridus Michx.
No specimens; apparently does not occur, although range given in Gray's *Manual* implies that it does.

Ruppia occidentalis Wats.
Does not occur; an apparently undescribed var. or subspecies of *R. maritima* L. from Big Stone Lake in the University collection is erroneously determined as *R. occidentalis.*

Najas guadalupensis (Spreng.) Morong.
Reported by Wheeler in Contributions to the Flora of S. E. Minnesota; report based on an incorrect determination.

Sagittaria subulata (L.) Buchenau.
Reported in Lapham's *Catalogue*, but does not occur.

Echinodorus tenellus (Martius) Buchenau.
Reported in Upham's *Catalogue* but does not occur. The report is probably based on some small specimen of *Sagittaria*.

Leptoloma cognatum (Schultes) Chase.
Reported in Upham's *Catalogue;* no specimens; occurrence very doubtful.

Panicum agrostoides Spreng.
Reported in Upham's *Catalogue;* no specimens.

Panicum depauperatum Muhl.
Various reports, but does not appear to occur; reports based on wrong determination of *P. perlongum* Nash. and *P. linearifolium* Scribn.

Panicum Werneri Scribn.
Reported in Wheeler's *Catalog*, but does not occur; report based on incorrect determinations.

Panicum dichotomum L.
Several reports, but does not occur; reports based on wrong determinations of other species.

Panicum implicatum Scribn.
Reported in Wheeler's *Catalog;* apparently confused with *P. villosissimum* Nash.

Panicum clandestinum L.
Assumed in Upham's *Catalogue* to occur; no specimens.

Panicum Boscii Poir.
Reported from Minnesota but all specimens originally so labelled are placed by Hitchcock and Chase in *P. latifolium* L. Several specimens, however, show the pubescence character of *P. Boscii* as given in recent descriptions, but most of the Minnesota plants have small spikelets and in this respect agree with *P. latifolium*. The two species do not appear to be sufficiently distinct.

Echinochloa Walteri (Pursh) Nash.
Doubtful whether it occurs; specimens in the University collection so determined are *E. Crusgalli* (L.) Beauv.

Setaria verticillata (L.) Beauv.
Reported in Upham's *Catalogue;* no specimens; it probably does not occur.

Anthoxanthum odoratum L.
Reported in Wheeler's *Catalog*. The report is based on incorrect determination of a single specimen of *A. Puellii* Lecoq. & Lamotte.

Stipa canadensis Poir.
Reported in Upham's *Catalogue;* no specimens; probably does not occur.

Stipa avenacea L.
Reported by Sheldon; report based on an incorrect determination of *S. comata* Trin. and Rupr.

Aristida dichotoma Michx. var. *Curtisii* Gray.
Reported in Wheeler's *Catalog;* report based on incorrect determination.

Aristida tuberculosa Nutt.
Reported in Lapham's *Catalogue,* and Britton & Brown's *Flora;* no specimens.

Aristida purpurascens Poir.
Reported in Lapham's *Catalogue;* no specimens.

Muhlenbergia sobolifera (Muhl.) Trin.
Reported in Lapham's *Catalogue;* no specimens in University collection.

Muhlenbergia tenuiflora (Willd.) B. S. P.
Reported in Lapham's *Catalogue;* no specimens.

Muhlenbergia Schreberi J. F. Gmel.
Reported by Sheldon in *Minnesota Botanical Studies:* the report is based on incorrect determinations of *M. mexicana* (L.) Trin.

Sporobolus asper (Michx.) Kunth.
Reported by Lapham; no specimens.

Sporobolus vaginiflorus (Torr.) Wood.
Reported in Upham's *Catalogue,* on collections of O. W. Oestlund; apparently is based on an incorrect determination.

Calamagrostis Pickeringii Gray var. *lacustris* (Kearney) Hitchcock.
No specimens in University herbarium; occurrence doubtful.

Calamagrostis cinnoides (Muhl.) Barton.
Reported in Lapham's *Catalogue;* no specimens; probably does not occur.

Calamagrostis Macouniana Vasey.
Reported in Wheeler's *Catalog of Minnesota Grasses;* report based on wrong determination of *C. canadensis* (Michx.) Beauv.

Ammophila arenaria (L.) Link.
Reported in Upham's *Catalogue* as occurring along the south shore of Lake Superior and inferred to occur in Minnesota; no specimens.

Spartina gracilis Trin.
Reported in Wheeler's *Catalog;* report based on incorrect determination of a specimen of *S. Michauxiana* Hitchcock from southwestern Minnesota.

Eragrostis Frankii (Fisch., Mey, and Lall.) Steud.
Reported in Upham's *Catalogue* on a collection by O. W. Oestlund; determination incorrect.

Melica mutica Walt.
Reported by L. H. Pammell from Houston County; no specimens,

though much botanical work has been done in that County; probably does not occur in the state.

Melica Smithii (Porter) Vasey.
Reported by Upham as probably occurring on the north shore of Lake Superior; no specimens.

Diarrhena diandra (Michx.) Wood.
Reported in Upham's *Catalogue* from Sherburne County; no specimens; probably does not occur.

Poa alpina L.
Reported from the north shore of Lake Superior; the specimens in the herbarium upon which some of these reports are made are all to be referred to *Poa glauca* Vahl.

Poa sylvestris Gray.
Reported in Upham's *Catalogue* from the southern and western parts of the state; no specimens; report probably incorrect.

Poa laevigata Scribn.
Reported by Arthur, Bailey and Holway from the Lake Vermillion region; report based on an incorrect determination of *P. nemoralis* L.

Glyceria Torreyana (Spreng.) Hitchcock.
Reported in Upham's *Catalogue;* no specimens; occurrence very doubtful.

Festuca rubra L.
No specimens.

Agropyron dasystachyum (Hook.) Scribn.
Reported in Upham's *Catalogue* as occurring on the north shore of Lake Superior, but probably does not reach Minnesota; no specimens.

Agropyron pseudorepens Scribn. and Sm.
Reported in Wheeler's *Catalog;* the report is based on incorrect determinations of *A. repens* (L.) Beauv. and *A. tenerum* Vasey.

Hordeum nodosum L.
Various reports; apparently all based on incorrectly determined specimens of *H. pusillum* Nutt.

Elymus glaucus Buckl.
Reported from the Red River Valley in Wheeler's *Catalog of Minn. Grasses;* report probably based on specimens of *E. Macounii* Vasey.

Elymus arenarius L.
Reported in Upham's *Catalogue* from the north shore of Lake Superior; no specimens; it is doubtful whether it occurs along the rocky north shore in Minnesota.

Sitanion longifolium J. G. Smith.
Reported (as *S. elymoides* Raf.) in Upham's *Catalogue* on a collection from Blue Earth County by Leiberg; probably a wrong determination; no specimens.

Cyperus Engelmanni Steud.
Reported by Holzinger and E. J. Hill; no specimens.

Cyperus alterniflorus Schw.
Reported in Lapham's *Catalogue* but does not occur.

Eleocharis intermedia (Muhl.) Schultes.
No specimens can be referred to this species without doubt, and the report seems to be based on incorrect determinations.

Scirpus nanus Spreng.
Report based on incorrect determinations.

Scripus hudsonianus (Michx.) Fernald.
Reported by Upham and others; no specimens.

Scirpus sylvaticus L.
Does not occur; report by Sheldon based on specimens of *S. rubrotinctus* Fernald.

Scirpus pallidus (Britton) Fernald.
Reported, but specimens in the University Herbarium are not sufficiently distinct from *S. atrovirens* Muhl. to be separated from the latter species.

Scirpus polyphyllus Vahl.
Reported by Upham from Isanti County; report based on incorrect determination of *S. atrovirens* Muhl.

Scirpus lineatus Michx.
Reported in Upham's *Catalogue;* no specimens.

Eriophorum tenellum Nutt.
Reported in Upham's *Catalogue;* report based on specimens of *E. gracile* Roth.; does not occur.

Cladium mariscoides (Muhl.) Torr.
No specimens; probably does not occur.

Carex foenea Willd.
All the specimens in the University herbarium labelled *C. foenea* are *C. aenea* Fernald.

Carex exilis, Dewey.
Reported by Sheldon in *Minnesota Botanical Studies;* the specimens in the herbarium so labelled are incorrectly determined; probably does not occur.

Carex conjuncta Boot.
Reported in Upham's *Catalogue;* no specimens.

Carex stenophylla Wahlenb.
Implied in Gray's *Manual* to occur; no specimens.

Carex bicolor All.
Reported from north shore of Lake Superior; no specimens.

Carex Davisii Schwein. and Torr.
Reported in Upham's *Catalogue;* no specimens; probably does not occur.

Carex albicans Willd.
Reported in Gray's *Manual;* no specimens.

Carex rariflora Smith.
Does not occur; report seems to be based on incorrect determination of *C. limosa* L.

Carex Richardsoni R. Br.
Reported in Upham's *Catalogue;* no specimens.

Carex Crawei Dewey.
Reported as in the range; no specimens.

Carex lurida Wahlenb.
Several reports; mostly based on incorrect determinations of *C. hystericina* Muhl; apparently does not occur.

Carex Schweinitzii Dewey.
Reported in Minnesota Metaspermae; one specimen in the University Herbarium labelled *C. Schweinitzii* is incorrectly determined; not likely to occur so far northwest.

Carex lupuliformis Sartwell.
No specimens are undoubted *C. lupuliformis;* generally confused with *C. lupulina* Muhl.

Carex retrorsa Schwein. var. *Hartii* (Dewey) Gray.
No specimens.

Wolffia punctata Griseb.
Reported in Minnesota Metaspermae; report based on incorrect determination of *W. columbiana* Karst.

Xyris montana Ries.
Reported from Lake Superior; no specimens.

Tradescantia virginiana L.
Reported in Britton and Brown's Flora to range from southern New York to South Dakota; none of the Minnesota specimens belong to this species, although many are so labelled; all have abundant glandular pubescence, and appear to be *T. bracteata* Small.

Tradescantia occidentalis (Britton) Smyth.
No specimens; probably does not occur.

Juncus acuminatus Michx.
Reported in Upham's *Catalogue;* report based on incorrect determinations.

Juncus articulatus L.
No specimens.

Juncus scirpoides Lam.
Reported in Lapham's *Catalogue,* but does not occur.

Melanthium virginicum L.
Reported in Upham's *Catalogue;* based on incorrect determination; does not occur.

Veratrum viride Ait.
Reported from Stearns County; no specimens.

Uvularia perfoliata L.

Apparently does not occur; all the Minnesota specimens in the University Herbarium labelled *U. perfoliata* are *U. grandiflora* J. E. Smith.

Allium Schoenoprasum L. var. *sibiricum* (L.) Hartm.

No specimens; doubtful whether it occurs.

Allium cernuum Roth.

Apparently does not occur; all specimens in the University Herbarium labelled *A. cernuum* are *A. stellatum* Ker.

Lilium superbum L.

This species has been reported from various parts of the state, but it seems that all these collections will have to be referred to *L. canadense* L. The lily common in our moist meadows and rich grounds seems to combine those characters utilized in the manuals and floras for separating *L. superbum* from *L. canadense*. The leaves have the rough margins and nerves of *L. canadense*, but the orange-colored flowers with the strongly reflexed perianth segments of *L. superbum*. Occasionally forms occur in which the nerves are almost smooth. The plant produces a rhizome about 7-10 cm. long, which by the end of July has developed a distinct bulb at the end with numerous close-set yellowish scales.*

Camassia esculenta (Ker) Robinson.

Reported from southern part of the state in Upham's *Catalogue;* no specimens; occurrence very doubtful.

Streptopus roseus Michx.

All previous reports of this species should be referred to *S. longipes* Fernald.

Medeola virginiana L.

No specimens; probably does not occur.

Trillium sessile L.

No specimens; probably does not occur.

Trillium recurvatum Beck.

No specimens; probably does not occur.

Trillium erectum L.

All reports of this species are to be referred to *T. declinatum* (Gray) Gleason.

Aletris farinosa L.

Reported in Lapham's *Catalogue;* no specimens; probably does not occur.

Smilax ecirrhata (Engelm.) Wats.

Confused with young specimens of *S. herbacea* L.; does not occur.

*Since this paragraph was written, O. A. Farwell has described two new species of *Lilium* from Michigan, *L. michiganense* and *L. peramoenum* (Bull. Torr. Bot. Club 42:351). All of the Minnesota specimens which have been called *L. superbum* and *L. canadense* appear to belong to these new species. To the present authors it appears from Mr. Farwell's descriptions, and the examination of many Minnesota specimens that the two proposed species are doubtfully distinct from one another.

Smilax rotundifolia L.
All reports of this species in the state based on incorrect determinations of *S. hispida* Muhl.

Sisyrinchium mucronatum Michx.
Report based on an incorrect determination of *S. angustifolium* Mill.

Sisyrinchium gramineum Curtis.
No specimens; probably does not occur.

Cypripedium passerinum Richards.
Reported from Lake Superior; no specimens.

Habenaria blephariglottis (Willd.) Torr.
Reported in Upham's *Catalogue* from near Duluth; no specimens; probably does not occur.

Spiranthes lucida (H. H. Eaton) Ames.
Reported in Upham's *Catalogue,* but does not occur.

Epipactis decipiens (Hook.) Ames.
Inferred to occur in Minnesota; no specimens.

Epipactis tesselata (Lodd.) A. A. Eaton.
Reported as far south and west as Lake Superior; no specimens.

Listera convallarioides (Sw.) Torr.
Reported in Upham's *Catalogue* as occurring between Lake Superior and Lake of the Woods; no specimens.

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